

THE TAXONOMY OF *CAREX* SECTION *STELLULATAE* IN NORTH AMERICA NORTH OF MEXICO

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INTRODUCTION

The genus *Carex* is one of the largest amphimictic genera of vascular plants with an estimated 1,000 (Hitchcock et al., 1969) to 2,500 (Nelmes, 1952a) species. While size alone does not necessarily indicate taxonomic difficulty, *Carex* is a genus that does often plague taxonomists. One of the most problematic sections in *Carex* is the *Stellulatae*. It should be noted here that the nomenclatural difficulties surrounding the infrageneric taxa in *Carex* are formidable (Voss, 1966). Because of this, the currently accepted nomenclature of the subdivisions of the genus (Mackenzie, 1931, 1935) is here followed without further comment.

As defined by Mackenzie (1931), section *Stellulatae* is best developed in eastern North America. Here Mackenzie recognized 16 species: *Carex echinata* Murray (*C. muricata* auct. non L.), *C. cephalantha* (Bailey) Bicknell, *C. angustior* Mackenzie, *C. laricina* Bright, *C. sterilis* Willdenow, *C. interior* L. H. Bailey, *C. exilis* Dewey, *C. josselynii* (Fernald) Pease, *C. elachycarpa* Fernald, *C. mohriana* Mackenzie, *C. atlantica* L. H. Bailey, *C. incompta* Bicknell, *C. howei* Mackenzie, *C. seorsa* E. C. Howe, *C. ruthii* Mackenzie, *C. wiegandii* Mackenzie. Some of these species he considered transcontinental. *Carex phyllomanica* W. Boott, *C. ormantha* (Fernald) Mackenzie, and *C. laeviculmis* Meinschausen were considered by Mackenzie to be endemic to western North America. One species, *C. townsendii* Mackenzie, was restricted to Mexico.

Outside of North America, *Carex echinata* is known throughout much of Europe (Jermy and Tutin, 1968) and also in the south temperate zone in New Zealand (Moore and Edgar, 1970) and Victoria and New South Wales, Australia (Moore, 1893; Ewart, 1930; Willis, 1970). *Carex omiana* Franch. & Savat., *C. echinata*, and *C. angustior* are reported from eastern Asia (Egorova, 1960, 1966; Ohwi, 1936). In addition, three species which have been referred to the *Stellulatae* are isolated endemics on tropical mountains: *C. gajonum* Nelmes (1952b) in Sumatra, *C. svenonis* Skottsberg (1944) in Hawaii and *C. peruleia* S. T. Blake (1947) in New Guinea.

In North America, there has been vast divergence in the taxonomic treatments of this group. In northeastern North America alone the number of species recently recognized has varied from nine (Gleason, 1952; Gleason and Conquist, 1963) to 14 (Fernald, 1950) and even 15 (Mackenzie, 1931). The number of species reported from Canada has varied from 12 (Mackenzie, 1931) to three (Boivin, 1967).

MATERIALS AND METHODS

This study was based on examination of about 8,000 specimens located in the following herbaria: ACAD, ALTA, CAN, CM, DAO, F, FLAS, GA, GH, MICH, MIN, NCU, NY, PH, QK, SHER, SIU, TEX, TRT, TRTE, UARK, UBC, UC, WIS. In addition, the species were studied in the field in Ontario from 1974 to 1977 and along the east coast of North America from Nova Scotia and southern Quebec to Massachusetts in 1975 and 1978.

Citations of representative specimens are available from the senior author upon request.

TAXONOMIC CHARACTERS

A wide variety of characters are available within the genus *Carex*. In compiling features for examination in this work, keys and descriptions in a number of previous treatments of this section were consulted. Especially useful in this respect were Mackenzie (1931), Hermann (1941), Fernald (1950), Gleason (1952), and Voss (1972), and more generally Damman (1964) and Jermy and Tutin (1968). In addition a thorough search was made for new features that might be of use.

The vegetative organs and flowers are rather simple; thus, most of the characters are concentrated in the inflorescence and infructescence. Fruiting characters specifically are used a great deal and, in this investigation, were unavoidably the most numerous character type. Nevertheless, the obvious utility of fruiting characters and the dubious success of vegetative keys except in relatively depauperate *Carex* floras (Damman, 1964; Jermy and Tutin, 1968) should not obscure the usefulness of some nonfruiting characters. In this investigation, leaf width, leaf section type, and distance between adjacent spikes on the culm were found to be quite useful.

As it is potentially of considerable significance, the precise manner in which some of the characters were measured will be briefly discussed. In the *Stellulatae*, perhaps the most critical decision is which perigynium should be measured. Many keys contain a general statement that the perigynia in the middle of the spike are most characteristic and should be used for comparison. A check on this initially obvious statement revealed that it is indeed not so obvious at all. It was evident that, at least in the *Stellulatae*, the perigynium length/width ratio is most different between species and least variable within a species on the lowest perigynia of the spikes. The middle and certainly the uppermost perigynia are more variable and, in fact, perigynia of all species converge in shape towards the apex of the spike so that they become essentially indistinguishable (Reznicek, 1978). If there are relatively few perigynia in the spike, often only the lowest one or two are suitable for measurement as characteristically developed for the species.

The perigynium beak was on occasion difficult to define. It was measured from the first inflection point in the curve at the transition from beak to body to the tip of the teeth at the apex of the beak. The width of the perigynium was always measured at the widest point, regardless of its location, and the number of nerves of the perigynium was counted over the achene on the adaxial surface above the basal spongy layer. Throughout the text the terms nerve and vein have been used interchangeably.

When leaves were measured, the largest culm leaf was always used. This was usually the uppermost leaf (except in *Carex exilis*). The widest leaf on the plant proved a significant character. In its measurement, all leaves were considered, including the dried up leaves of the previous year. These old leaves, usually produced on sterile shoots after the plants have fruited, are sometimes much larger than culm leaves and, as is the case with the shape of the lowest perigynia on a spike, better express the potential variation of the plant. For this reason, plants of this group should not be cleaned of their dead leaves when preparing specimens.

RELATED SECTIONS AND LIMITS OF THE *STELLULATAE*

It is clear that a complete revision of group boundaries even in one section of *Carex* like the *Stellulatae* cannot be attempted without examination of world-wide material which is beyond the scope of this work. However, some discussion of relationships and minor realignments of North American species seems necessary at this point.

The *Stellulatae*, as defined by Mackenzie (1931), are close to three other sections of *Carex* in North America: the notoriously difficult *Ovales*, the boreal *Heleonastes*, and the primarily woodland *Deweyanae*. These groups and the *Stellulatae* all have in common gynecandrous, simple spikes and a usually cespitose habit. The *Ovales* characteristically have more or less scale-like perigynia appressed and more or less overlapping in a dense head. The perigynia are thin-margined, sometimes even winged and often stramineous. The *Heleonastes*, excluding *C. disperma* Dewey (Ohwi, 1936; Toivonen and Timonen, 1976), characteristically have short-beaked or essentially beakless, plump, ascending to spreading perigynia that are not spongy-thickened at the base and usually appear minutely whitish punctulate. The *Deweyanae* have ascending or even appressed-ascending perigynia. The plants themselves have a lax and spreading habit. The *Stellulatae* are characterized by spreading to reflexed perigynia that are prominently beaked, spongy at base, thick-margined, not white punctulate and with a usually serrulate beak.

As Mackenzie (1931) defined the section, the *Stellulatae* included 20 species in North America. In addition, a few other North American species have been included in it in the past. *Carex gynocrates* and its relatives, now placed in the *Dioicae*, were placed here by Fernald (1902) and Holm (1903) but these differ strongly in being much smaller, slender, delicate, dioecious mat-formers. *Carex illota* was included by Mackenzie (1917, 1922) but later aligned with the *Ovales* (Mackenzie, 1931). Moore and Calder (1964) concurred with this placement. Since the species has more or less sharp-edged, ascending perigynia without a spongy base and a smooth-margined beak that is not bidentate, the plant certainly does not belong in the *Stellulatae*.

Mackenzie (1931) separated the *Stellulatae* from the *Deweyanae* by "perigynia spreading or ascending at maturity" for the former contrasted with "perigynia appressed" for the latter. However, Mackenzie included three species in the *Stellulatae* which differed considerably from the above description: *Carex laeiculmis*, which was described as having perigynia "appressed or ascending," *C. elachycarpa* with perigynia "closely appressed," and *C. josselynii* with perigynia "appressed-ascending." The taxonomic position of *C. josselynii* and *C. elachycarpa*, considered endemic to northern Maine, has already been discussed (Reznicek and Ball, 1979) and they were shown to be based on abnormal individuals of species with normally spreading to reflexed perigynia. *Carex laeiculmis*, on the other hand, is a widespread species of western North America ranging from Alaska to California. In addition to appressed or ascending perigynia, it has a lax, spreading habit. These characteristics, along with its overall aspectual similarity to *C. deweyana* and *C. bromoides*, place it clearly with the *Deweyanae*, not the *Stellulatae*. As it was at one time described as a variety of *C. deweyana* (Bailey, 1888), it is difficult to understand Mackenzie's placement of it in the *Stellulatae* without any mention that it was unusual in the group. Fernald (1902) noted that it was similar to *C. seorsa* in having a smooth-beaked perigynium and this may have been partly responsible for Mackenzie's decision. It is here considered as a member of the *Deweyanae* and will not be discussed further.

The exclusion of *Carex laeiculmis* from the *Stellulatae* leaves a uniform group of cespitose sedges with gynecandrous spikes of widely spreading to reflexed perigynia that are planoconvex to more or less biconvex, thick-margined, and have a prominent serrulate, bidentate beak and spongy base. Only three species differ slightly from this description.

Carex exilis has involute leaves and usually solitary spikes. It may also occasionally be dioecious. These features have led to its placement in the *Dioicae* by some authors (Tuckerman, 1843; Kükenthal 1909). This placement was also supported by Savile and Calder (1953) using evidence derived from the phylogeny of *Carex*-infecting smuts. Comparison of micromorphological features of the perigynium and achene epidermis of *C. exilis* with *C. echinata*, *C. interior*, *C. dioica* L. and *C. parallela* (Laest.) Sommerf. was

also interpreted as providing support for the placement of *C. exilis* in the *Dioicae* (Toivonen and Timonen, 1976). However, *Carex exilis* is not normally dioecious and may be multiple-spiked. Additionally, characters of the perigynium such as shape, beak-toothing and marginal serration are those of the *Stellulatae*. Multiple-spiked individuals, save for involute leaves, very closely resemble other species of *Stellulatae* and would seem to indicate a close relationship of *C. exilis* to the *Stellulatae* rather than to the normally dioecious and exclusively single-spiked *Dioicae*. This relationship has been noted by several authors (Boott, 1858; Holm, 1901, 1903; Nelmes, 1952a). *Carex exilis* is here placed in the *Stellulatae* pending further evidence from additional characters and examination of other relevant species in the *Dioicae*. With its stiff involute leaves and usually single spikes, *C. exilis* is a plant of striking appearance and is here regarded as a specialized and somewhat isolated species within the group.

Carex sterilis differs slightly in being incompletely or even completely dioecious. In all other features it is very similar to other species of *Stellulatae*. Dioecious *Carex* are rare and most have single spikes. The only other more or less dioecious, multiple-spiked *Carex* known to the authors in North America are several species in the *Divisae* (MacKenzie, 1931; Reznicek, Catling, and McKay, 1976; Hudson, 1977). It should be noted here that most keys to *Carex* segregate the *Stellulatae* using the gynecandrous nature of the spikes, especially the terminal spike. Clearly, *C. sterilis* cannot be keyed correctly using this feature.

Carex seorsa, while of typical sex distribution and spike number, differs slightly in having a smooth perigynium beak with the widest part of the perigynium only slightly below the middle.

The remaining species of *Stellulatae* are all extremely similar in morphology. Thus, even with the rather specialized *Carex exilis*, the group is a very uniform and well defined natural taxon.

THE DELIMITATION OF SPECIES IN SECTION *STELLULATAE*

While the *Stellulatae* as a whole present extreme taxonomic difficulties, there nevertheless are some taxa that are distinctive. In dealing with the taxonomy of the group it is best to discuss these distinctive plants first and leave the problem areas for detailed discussion.

The most distinctive member of the *Stellulatae* is *Carex exilis*. It is amply distinguished from all other members by its usually single spike (Fig. 36), involute, stiff leaves, and large anthers.

Carex seorsa is also a distinctive species. It is a more or less lax plant with soft leaves contrasting with the often stiff clumps of the other species. It is unique in the *Stellulatae* in having a totally smooth-margined beak. The perigynium is also widest closer to the middle and has a more tapering base than most individuals of other species. The perigynium is not, however, widest near the middle as described by numerous authors. Figures 1 and 35 both illustrate that it is in fact usually widest somewhat below the middle. The plant also usually has a shorter beak and longer ligule than other members of the *Stellulatae*.

Carex sterilis is a most interesting species. It was the first exclusively American species to be described (Willdenow, 1805). In some recent works it is not recognized (Boivin, 1967) or only recognized at varietal level (Gleason, 1952; Gleason and Cronquist, 1963). Nevertheless, the plant is quite distinct from all other members of the *Stellulatae*. It is striking that in an overwhelming majority of cases the terminal spike is strongly unisexual, being either all pistillate with rarely 1 or 2 staminate flowers at the base or all staminate with rarely a few pistillate flowers. Virtually never does the terminal spike have the clavate base formed by staminate flowers that is so characteristic of all other members of the *Stellulatae* (Fig. 37). The lateral spikes are also strongly unisexual but

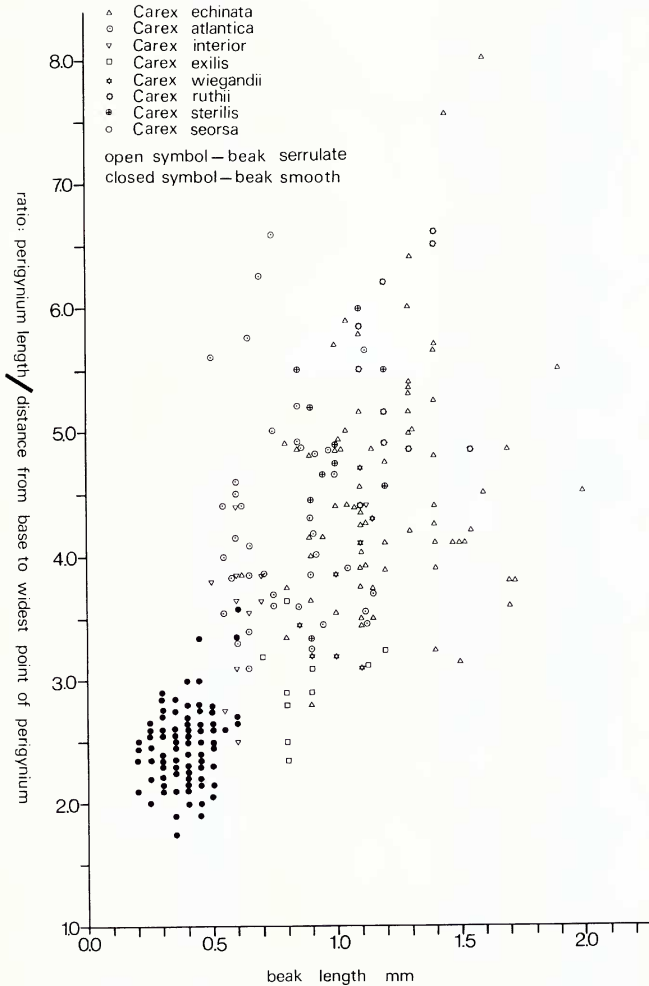


FIG. 1. Ratio of perigynium length and distance from base to widest point of perigynium plotted against beak length for *Carex echinata*, *C. atlantica*, *C. interior*, *C. exilis*, *C. wiegandii*, *C. ruthii*, *C. sterilis* and *C. seorsa*.

less so than the terminal spike. *Carex sterilis* does not have a regular arrangement of male and female flowers even on one spike and often the plants are more or less completely dioecious. Both these features, as noted before, make keying the species very difficult. Staminate specimens are particularly difficult to place if not recognized to species. A helpful clue (see key) is that they have larger anthers than most other species of *Stellulatae*. *Carex sterilis* also has more or less obtuse pistillate scales that are strongly castaneous with a usually broad hyaline tip and margin and usually castaneous perigynia with soft, hyaline-bordered teeth. These features also help separate it from other species in the group, which usually have lighter coloured perigynia and scales.

The remaining species are much more difficult. The correlations among characters are more obscure and the aspect of all species is quite similar. A close examination of leaf widths disclosed that the widest leaves found in the group, about 5 mm, were confined to two geographical regions and that certain morphological features were correlated with the leaf widths in each of the two areas. The two units correspond to Mackenzie's (1931) species *Carex ruthii*, confined to the southern Appalachian mountains, and *C. wiegandii*, whose range was centered about the Gulf of St. Lawrence. The two taxa are easily separated from one another by their distinctive infructescence structure (Fig. 2). *Carex ruthii* has an extremely open, elongate infructescence with considerable space between the lowest spikes (Fig. 43) whereas *C. wiegandii* has a dense, in some cases almost capitate, infructescence with even the lowest spikes closely approximate (Fig. 39). Further examination indicated that these two taxa can possess leaves as narrow as 2.8 mm in some cases, thus overlapping with *C. echinata* and *C. atlantica* which may occasionally have leaves broader than 2.8 mm (but never up to 5 mm). *Carex echinata* can easily be separated from *C. wiegandii* and *C. ruthii* by its longer, often acute pistillate scales. Both *C. ruthii* and *C. wiegandii* have shorter, more or less obtuse pistillate scales. Figure 3 shows clearly that the pistillate scale length of broad-leaved individuals of *C. echinata* is greater than that for specimens of *C. ruthii* and *C. wiegandii* with comparable leaf widths. Broad-leaved individuals of *C. atlantica* can usually be separated from *C. ruthii* and *C. wiegandii* by the extremely broad perigynia, normally 2 mm or more wide and 1.1 to 1.6 times as long as wide as shown in Fig. 4. In the rare case of overlap of features, the distinctive infructescence and restricted distribution of *C. ruthii* and *C. wiegandii* help to distinguish them.

Carex echinata and *C. atlantica* are, for convenience, treated as part of the narrow-leaved segment of the *Stellulatae* though they may sometimes have leaves greater than 2.8 mm wide. This group is by far the most variable and difficult.

Throughout the midwestern states and the southern Canadian prairie provinces there occurs only one species of *Stellulatae*. This is the common plant with diminutive spikes of small, short-beaked perigynia appropriately described by Bailey (1893) as *Carex interior*. This plant is remarkably uniform throughout its extensive range, which proved to include all provinces and territories of Canada, most of the northern and western United States, and Mexico south to the vicinity of Mexico City. *Carex interior* can sometimes be difficult to separate from related species where they are sympatric. However, from *C. echinata* it is relatively easily distinguished by beak length (Fig. 5). In the rare case of ambiguity, other less reliable features must be used, for example, the perigynium beak/body ratio, perigynium length/width ratio, venation of the perigynia, and the nature of the pistillate scales as outlined in the key and descriptions. *Carex interior* is much more difficult to separate from small plants of *C. atlantica*. The perigynia of *C. interior* have a distinctive shape. The sides are nearly straight to slightly convex and, in the taper to the beak, there is mostly a "shoulder" or second inflection point before a final concave taper. This "shoulder" is well illustrated by Boott (1858, *sub C. stellulata* var. *scirpoides*) who obviously clearly understood this plant. Nevertheless, it is a subtle distinction and easily missed if one is not familiar with this character. In addition, the perigynia of *C. interior* are usually nerveless on the adaxial surface whereas those of

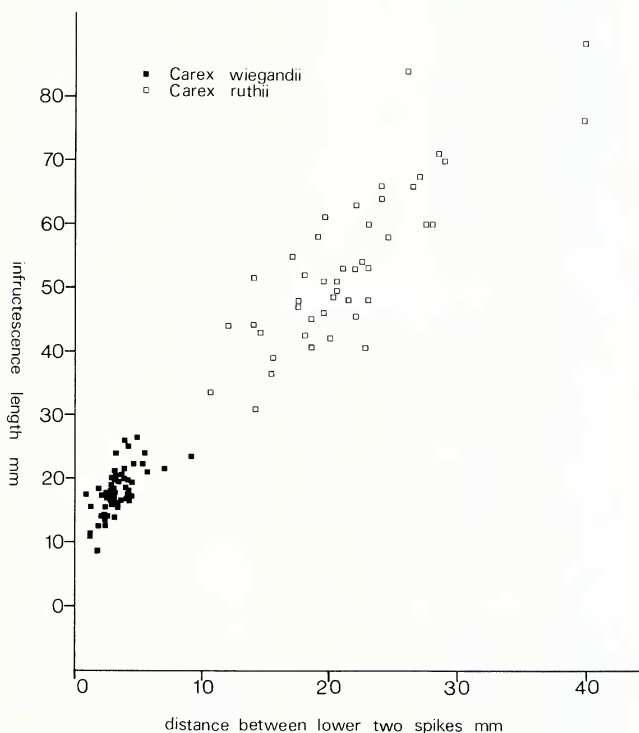


FIG. 2. Scatter plot of infructescence length and distance between the lower two spikes for *Carex ruthii* and *C. wiegandii*.

C. atlantica are usually nerved. *Carex interior* also usually has brownish or somewhat castaneous perigynia when mature while those of *C. atlantica* are usually greenish except when overripe. As well, on the beak and up to 1.0 mm below, the margins of the perigynia of *C. interior* are usually densely serrulate and often more or less setulose. The marginal teeth of *C. atlantica* are more sparse, arising singly and often with discernible space between the teeth. The perigynia of *C. interior* are 1.4–2.0 (2.2) times as long as wide and those of *C. atlantica* are 1.1–1.7 (1.9) times as long as wide. Although there is great overlap, this feature is helpful in separating specimens that may be ambiguous for some other features. Some of these features are illustrated in Fig. 6, which shows both the difficulty of separating the two species and that two groups are indeed present.

Including *Carex echinata* and *C. atlantica*, not yet discussed except as they related to species already mentioned, 11 species recognized by Mackenzie (1931) still remain to be dealt with. These are *C. atlantica*, *C. echinata* (*C. muricata* auct. non L.), *C. mohriana*, *C. howei*, *C. incompta*, *C. laricina*, *C. cephalantha*, *C. phyllomanica*, *C. ormantha*, *C. angustior*, and *C. townsendii*. When specimens representing this group of names were carefully analyzed, it was found that they fell into two clear-cut groups based on perigynium length/width ratios, beak length, perigynium colour, beak/body ratios, geographic distribution, and other features. The perigynium length/width ratio and beak length for the two groups are illustrated in Fig. 7. The group with longer, narrower perigynia with length/width ratios ranging from 1.75–3.6 and beak lengths from 0.85–2.05 mm includes *C. echinata*, *C. laricina*, *C. phyllomanica*, *C. ormantha*, *C. angustior*, *C. cephalantha*, and *C. townsendii*. The group with broader perigynia 1.1 to 1.9 times as long as wide and beaks 0.45 to 1.25 mm long includes *C. atlantica*,

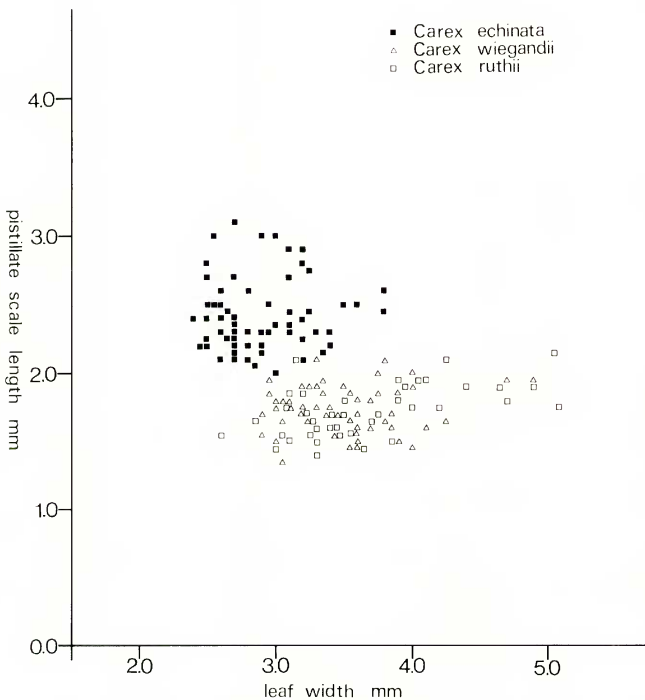


FIG. 3. Scatter plot of pistillate scale length and maximum leaf width for *Carex ruthii*, *C. wiegandii* and broad-leaved individuals of *C. echinata*.

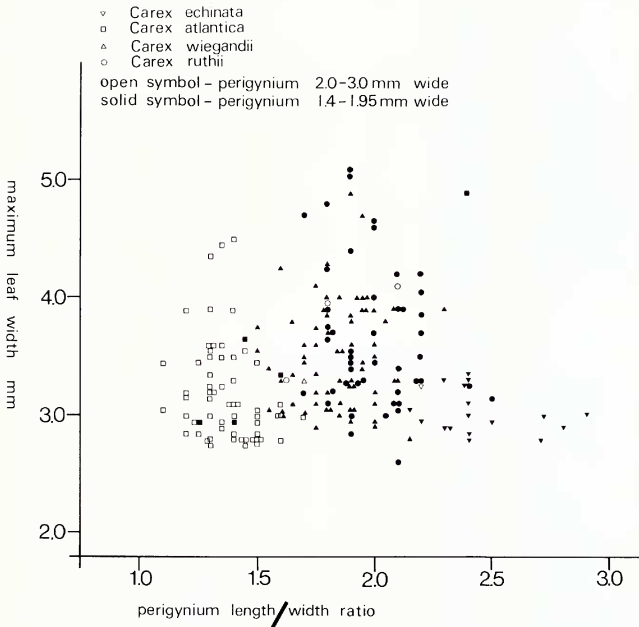


FIG 4. Perigynium length/width ratio plotted against maximum leaf width for *Carex ruthii*, *C. wiegandii* and broad-leaved individuals of *C. echinata* and *C. atlantica*.

C. mohriana, *C. incompta*, and *C. howei*. Only the names *C. echinata* and *C. atlantica* appear on Fig. 7 and it will be convenient to refer to the *C. atlantica* complex and the *C. echinata* complex containing respectively the names associated in the two groups listed above.

The *Carex atlantica* Complex

The four taxa in the *Carex atlantica* complex, *C. atlantica*, *C. incompta*, *C. howei*, and *C. mohriana*, were separated on the basis of perigynium size, infructescence length, leaf width, pistillate scale length and acuteness, and geographical distribution among other features. In Mackenzie's (1931) monograph, they fell into two groups. *C. howei* and *C. mohriana* were separated from *C. atlantica* and *C. incompta* by the key couplet "perigynia small, 2.25-3.25 mm long, the beak very shallowly bidentate one fourth to one third length of the body; scales half to two thirds length of bodies of perigynia" for *C. howei* and *C. mohriana* versus "perigynia 2.75-4.75 mm long, with beak sharply bidentate and ventral false suture conspicuous" for *C. atlantica* and *C. incompta*. Fig. 8 shows a frequency diagram of perigynium length for the complex. It is evident that

perigynium length is a unimodal curve with the mean of this sample being 2.75 mm. Careful examination of perigynium beak teeth indicated that in the *C. atlantica* complex, the length of the teeth is closely correlated with beak length and both correlate closely with perigynium size and follow the same pattern as shown in Fig. 8.

Carex mohriana was separated from *C. howei* by the couplet "spikes strongly separate; leaf-blades 0.25–1 mm wide" for *C. howei* and "spikes aggregated in a dense head; leaf-blades 1–2.5 mm wide" for *C. mohriana*. Examination of a wide selection of material showed that plants with densely aggregated spikes are of sporadic occurrence throughout the range of the *C. atlantica* complex and also occur through the entire range of leaf widths shown by the complex. Mackenzie (1931) considered the plant a central Florida endemic. Close inspection has not revealed any further diagnostic features. Isotypes of *C. mohriana* have some culms with elongate heads typical of the *C. atlantica* complex as a whole mixed with culms with dense heads. This segregate is a slight variant not worthy of recognition.

The separation of *Carex incompta* and *C. atlantica* has been discussed by Hermann (1965). He summarized key characters from various treatments, concluded that the two taxa were conspecific, and reduced *C. incompta* to varietal status as *C. atlantica* var. *incompta* (Bicknell) Hermann. Further to this end, a comparison has been made of two of the major key differences noted by Hermann (1965), the proportionate lengths of pistillate scale and perigynium body and the leaf width. *Carex incompta* is described as having the pistillate scales two-thirds to fully as long as the body of the perigynium and leaves 1.5 to 2.5 mm wide and *C. atlantica* as having the pistillate scales half to two-thirds the length of the body and leaves 1.5 to 4.0 mm wide. Figure 9 clearly shows that the variation in leaf width is hardly correlated with that of the pistillate scale length/perigynium body length proportion. Two groups cannot be sorted out here. As all other characters examined followed the same pattern, it would

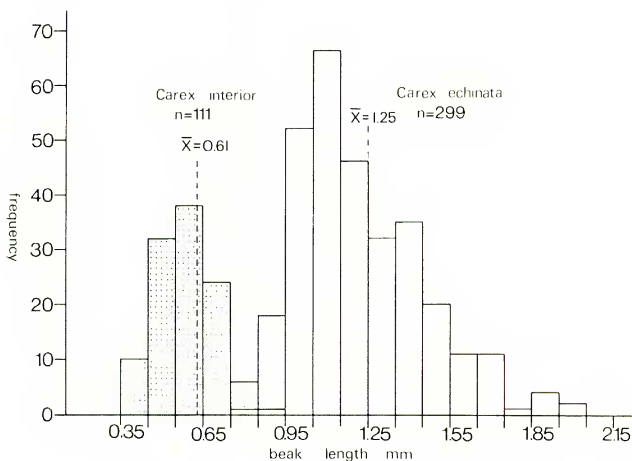


FIG. 5. Frequency diagram of beak length for *Carex interior* and *C. echinata*.

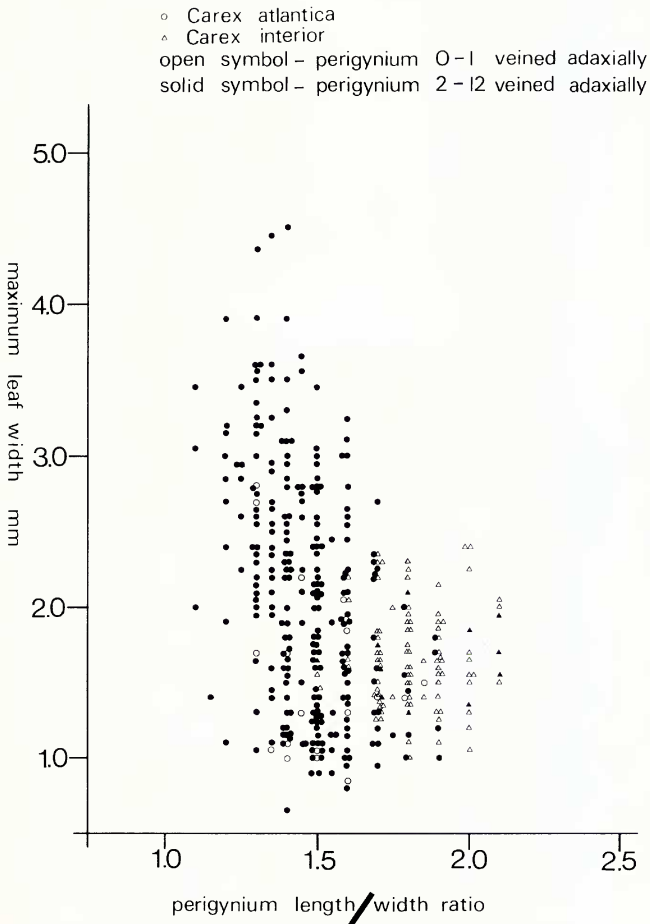


FIG. 6. Scatter plot of perigynium length/width ratio and maximum leaf width for *Carex atlantica* and *C. interior*. Disposition of specimens as *C. atlantica* or *C. interior* based on other features as noted in text.

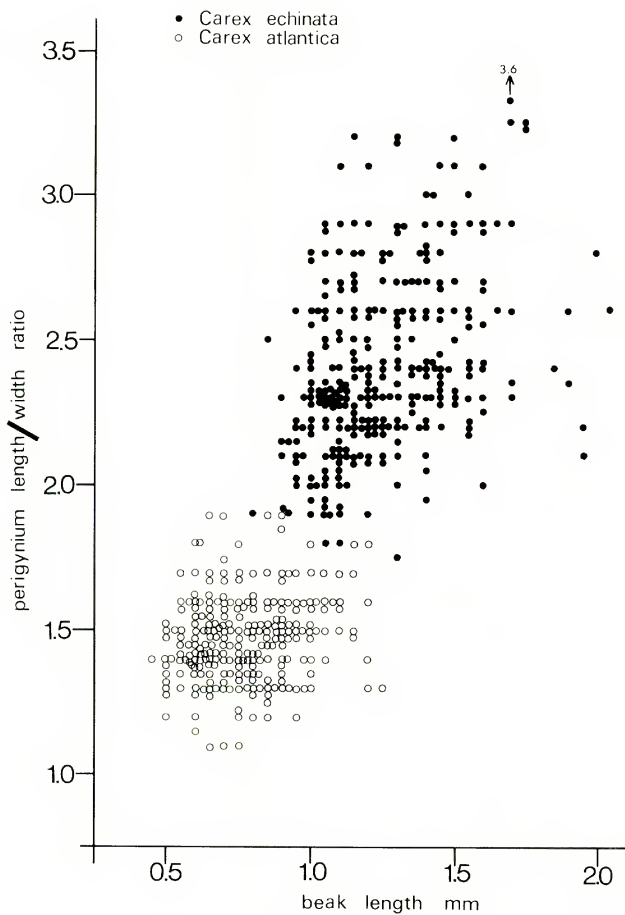


FIG. 7. Beak length plotted against perigynium length/width ratio for *Carex echinata* and *C. atlantica*.

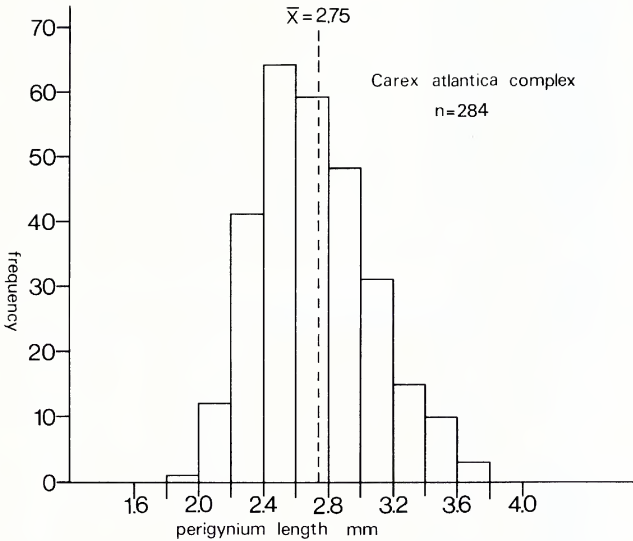


FIG. 8. Frequency diagram of perigynium length for *Carex atlantica*.

seem that *C. atlantica* and *C. incompta* are certainly conspecific as shown by Hermann (1965) and, more than that, not even different at varietal level.

One of the most interesting aspects of this study was the investigation of the relationships of *Carex howei*. From the time the taxon was first described by L. H. Bailey (1893), as *C. interior* var. *capillacea*, to the present, all authors in their keys, descriptions, and discussions have associated this species with *C. interior*. No mention was ever made of precisely how the plant was to be separated from *C. incompta* and *C. atlantica* except for the standard key characters noted before. We discovered that not only is the true relationship of *C. howei* with *C. atlantica* and its relatives, but in fact it is conspecific with them and not closely related to *C. interior* at all. The differences between *C. interior* and the *C. atlantica* complex have been discussed already. Plants fitting the description of *C. howei* have usually green perigynia 1.1 to 1.7 (–1.9) times as long as wide, veined on the adaxial surface with margins of beak and upper portion of body sparsely serrulate and no “shoulder” as described for *C. interior*. This is clearly in line with plants described as *C. atlantica* and *C. incompta*. Figure 6 shows leaf width plotted against perigynium length/width ratio for *C. interior* and the *C. atlantica* complex. Narrow-leaved (less than 1.6 mm wide) plants of the *C. atlantica* complex fit the description of *C. howei*. One can see here that they generally fit into the pattern of variation shown by the rest of the *C. atlantica* complex rather than fitting with the “bulge” shown by *C. interior*. *Carex howei* clearly represents the smallest variants of the *C. atlantica* complex and is not related to *C. interior*. Figure 10, perigynium length plotted against perigynium width, was coded for leaf widths that correspond to the

description of the three taxa. The maximum leaf width given in keys for *C. howei* was 1.0 mm (Fernald, 1950; Gleason and Cronquist, 1963; Voss, 1972) and the range for *C. incompta* 1.5 to 2.5 mm and for *C. atlantica* 1.5 to 4.0 mm (Mackenzie, 1931; Hermann, 1965). However, there are quite a number of plants of the *C. atlantica* complex with maximum leaf widths between 1.0 and 1.5 mm. Thus, the limits used on the graph were adjusted according to measurements of herbarium specimens determined by Mackenzie. Plants named *C. howei* often had leaves to 1.6 mm wide for even slightly wider in rare instances as pointed out by Voss (1972). The two larger groups, representing *C. atlantica* and *C. incompta*, also had their limits adjusted according to measurements of herbarium specimens as above. It can be seen here that rather than the presence of two or three taxa, the graph again shows a uniform pattern of variation for the entire

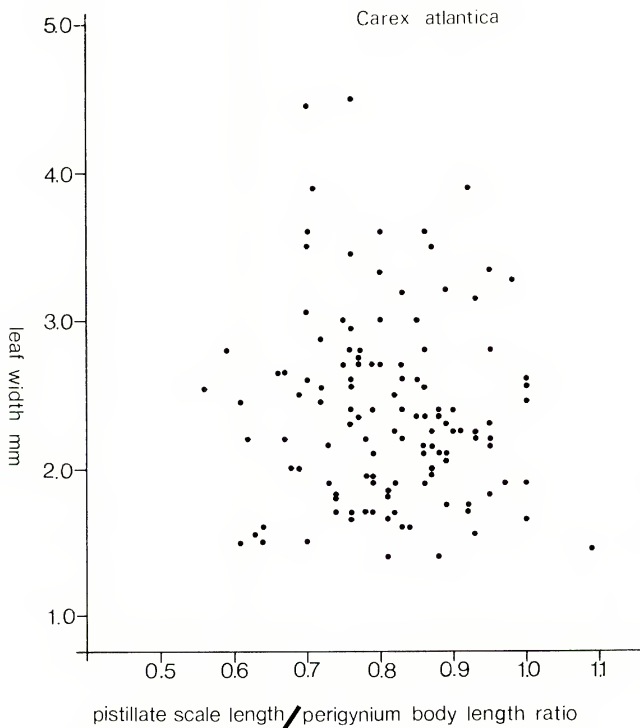


FIG. 9. Maximum leaf width plotted against ratio of pistillate scale length and perigynium body length for *Carex atlantica*.

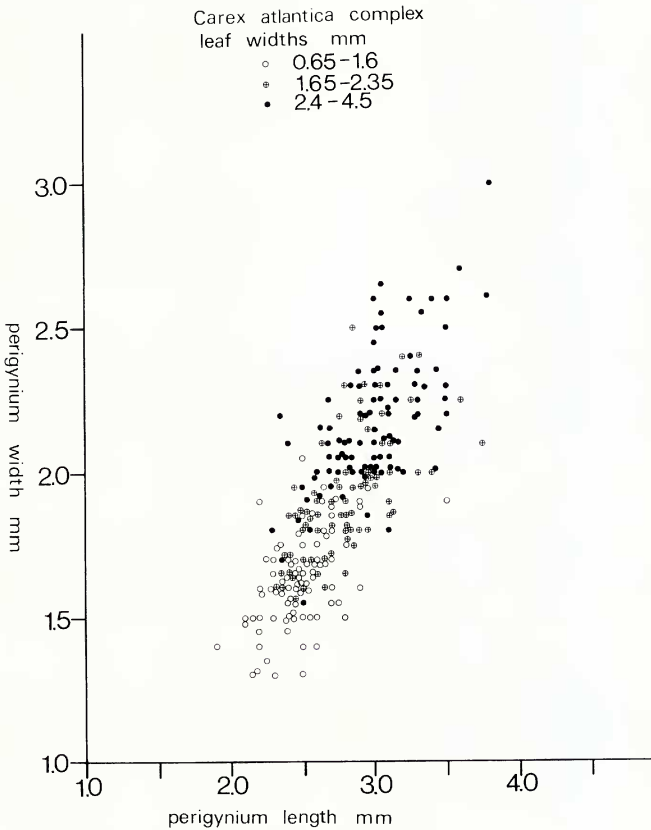


FIG. 10. Scatter plot of perigynium length and perigynium width for *Carex atlantica*.

C. atlantica complex and, obviously, that smaller plants have smaller perigynia but of the same shape. Again on this graph, as noted on Fig. 6, plants answering the description of *C. howei* are at the smallest end of the uniform variation spectrum shown by the *C. atlantica* complex just as plants called *C. atlantica* form the large end and *C. incompta* the middle. However, no discontinuities are detectable. The unimodal nature of the distribution of perigynium lengths has already been demonstrated (Fig. 8). Figure 6 also

clearly shows that there are many plants with leaves 1.0 to 1.5 mm wide, as pointed out previously.

However, the situation is not as simple as presented thus far. Although there is a lack of discontinuities in the *Carex atlantica* complex, characters show a definite segregation on a geographical basis. This is especially true for leaf width. Figure 11 demonstrates this differing abundance graphically for two areas, Nova Scotia and Georgia. In Nova Scotia, plants with widest leaves 1.5 mm to 1.9 mm are quite rare and a definite discontinuity of variation exists, whereas in Georgia a unimodal curve is indicated.

The taxonomic disposition of this kind of variable complex is always exceedingly unsatisfactory. This is especially so here since taxonomists working in local areas, for example Nova Scotia, will find "distinct" taxa because the total range of variability of the complex is not expressed throughout its entire range. Thus, a revision of the taxonomy based on specimens from a local area may well give different results from one including the entire range of the complex.

From the discussion above, it is evident that there is only one taxon at the species level in the *Carex atlantica* complex. Although the complex patterns of variation within that species are describable, they are very difficult to fit into the standard taxonomic hierarchy. It is felt that intergradation between plants fitting the description of *C. incompta* and *C. atlantica* is so complete over such a large area that recognition of two taxa, even at varietal level as proposed by Hermann (1965), is not feasible. Because the fine-leaved plants, fitting the description of *C. howei*, form recognizable populations with a distinctive distribution (Fig. 22) that may grow with broad-leaved plants without intergradation, they are here recognized at subspecific level as *C. atlantica* subsp. *capillacea*.

The *Carex echinata* Complex

Seven species were recognized by Mackenzie (1931) in the *Carex echinata* complex: *C. echinata* (*C. muricata* auct. non L.), *C. ormantha*, *C. phyllomanica*, *C. townsendii*, *C. angustior*, *C. laricina*, and *C. cephalantha*. *Carex townsendii* was described from Chihuahua, Mexico, but so few Mexican specimens of this complex have been examined that no further treatment is here possible.

The *Carex echinata* complex is widely distributed both on the eastern and western sides of the continent. In the east, the group has a more or less continuous range from Newfoundland and Labrador to western Ontario south to New Jersey, Iowa, and in the Appalachian mountains to southern North Carolina. In the west, the complex occurs on mountain chains and along the coast from Alaska to southern California and Colorado and again in Mexico. Specimens from the interior boreal region are extremely few. Of the species recognized by Mackenzie (1931) only two, *C. phyllomanica* and *C. ormantha*, were considered exclusively western North American and one, *C. laricina*, exclusively eastern North American. *Carex cephalantha*, *C. angustior*, and *C. echinata* were considered to occur on both sides of the continent. *Carex laricina* has, however, been united by recent authors with *C. cephalantha* (Fernald, 1950; Voss, 1972). Furthermore, the original description of *C. ormantha*, as *C. echinata* var. *ormantha* Fernald (1902), included Rhode Island and Connecticut plants. This leaves only *C. phyllomanica* considered as exclusively western by all authors.

Mackenzie's major division of these seven species was based on the nature of the pistillate scales. *Carex echinata*, *C. ormantha*, and *C. phyllomanica* were considered to have "obtuse or obtusish" scales, chestnut brown with bright white margins, not sharply keeled and with the midvein obscure at the apex. *Carex angustior*, *C. cephalantha*, and *C. laricina* were described as having pistillate scales "obtusish to cuspidate," yellowish brown with a narrow, opaque or dull white margin and a midvein prominent to the apex. When the pistillate scales were closely examined, they were found to be tremendously

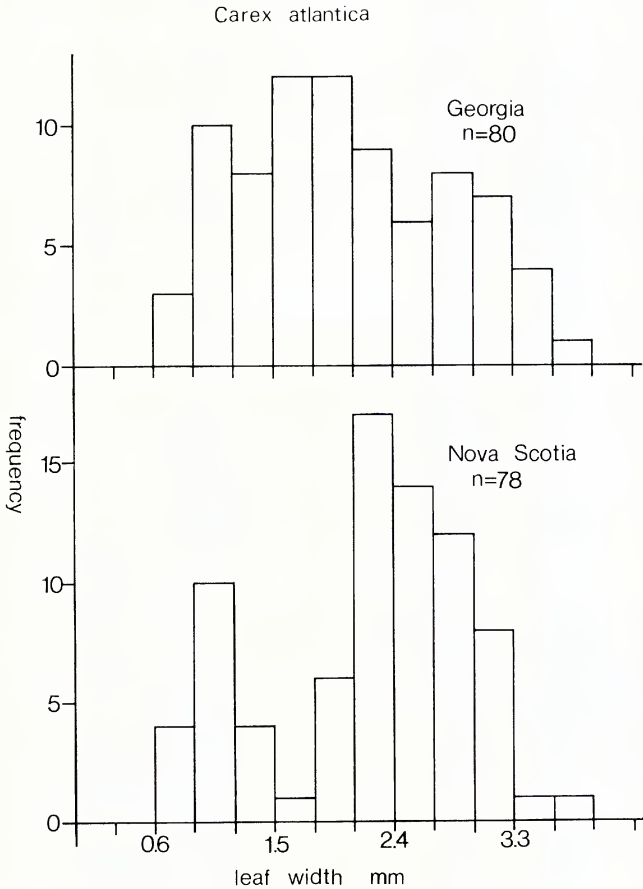


FIG. 11. Frequency diagrams of maximum leaf width for all specimens examined of *Carex atlantica* from Georgia (above) and Nova Scotia (below).

variable, both on the same spike and between plants. The variability on a single spike paralleled that of the perigynia as discussed earlier and variability between plants ranged more widely, even with plants of similar appearance. A brief survey of plants named *C. ormantha*, *C. phyllomanica*, and *C. echinata* by Mackenzie revealed that, of 23 examined, 7 had primarily obtuse or "obtusish" scales and 16 had mostly acute scales. In the same manner, an examination of 26 plants of *C. angustior*, *C. cephalantha*, and *C. laricina* disclosed 23 with acute scales and 3 with obtuse or "obtusish" scales. Variability of even greater magnitude crossing Mackenzie's specific boundaries was observed in the venation and bordering of scales.

Carex echinata was separated from *C. ormantha* and *C. phyllomanica* by its ovate perigynium and nerveless adaxial surface as contrasted with a many-nerved adaxial surface and "narrower" perigynia. When actual measurements and observations were made, the circumstances under which this separation was derived became puzzling for, of 74 specimens named *C. ormantha* and *C. phyllomanica*, including a considerable proportion named by Mackenzie himself, 20 were nerveless or with one faint nerve and 54 were 2-11-nerved. In addition, the perigynium length/width ratio ranged from 1.95 to 3.2 (3.6) times as long as wide. These values entirely encompassed those obtained for "authentic" *C. echinata*. The problems do not end here for, in distinguishing *C. ormantha* and *C. phyllomanica*, Mackenzie (1931) relied on the separation of the spikes in the infructescence and perigynium length. *Carex ormantha* was described as having a very open infructescence and perigynia 3.5 to 4.0 mm long and *C. phyllomanica* a very dense infructescence and perigynia 3.75 to 4.5 mm long. The best way found to express the nature of the differences was to use the ratio of culm length/infructescence length. Figure 12 shows how the two classes of plants segregate with regard to these two characters. It can be readily seen that the separation is anything but clear-cut. Perigynium length and infructescence density do not correlate well at all. Although the dense-headed plants are primarily coastal, the separation of the two taxa on these characters at specific level is not feasible. As well, western plants fitting the descriptions of *C. cephalantha*, *C. echinata*, and *C. angustior* were excluded from the graph. They are somewhat intermediate between *C. phyllomanica* and *C. ormantha* for these characters.

A close examination of *Carex angustior*, *C. laricina*, and *C. cephalantha* is also in order. *Carex angustior* was considered to have very narrow, lanceolate perigynia nerveless on the adaxial surface with a beak equalling or exceeding the length of the body and the achene much longer than wide. Both *C. laricina* and *C. cephalantha* were described as having perigynia ovate, the beak much shorter than the body, the achenes about as wide as long, and perigynia nerved on the adaxial surface. Figure 13 shows the pattern of beak length/body length ratio, number of nerves on the adaxial surface, and perigynium length/width ratio for the *C. echinata* complex. In this revealing figure, it can be seen that perigynium beak/body ratio, perigynium length/width ratio, and the number of nerves on the adaxial surface of the perigynium are only loosely correlated. Certainly, no discontinuous clusters of variation are evident. In addition, variation in these characters in the east of North America is nearly paralleled by that in the west. At the very least, if there are separate species in the complex, they cannot be distinguished using these features. However, it is notable that the plants with the narrowest perigynia were both invariably nerveless and from the east. The achene length/width ratio could not be placed on Fig. 13 without confusion but it shows parallel variation to the perigynium length/width ratio in the *C. echinata* complex. *Carex angustior* was also characterized as being a delicate plant with narrow leaves and a dense infructescence (Mackenzie, 1931) but these characters also show great variability.

Carex cephalantha and *C. laricina* have been united by a number of authors (Fernald, 1950; Voss, 1972). Mackenzie (1931) separated the two mainly on the basis of perigynium length. *Carex laricina* he indicated had perigynia 2.75 mm to 3.5 mm long and *C. cephalantha* 3.5 mm to 4.0 mm long. Hermann (1941), adjusted the range of

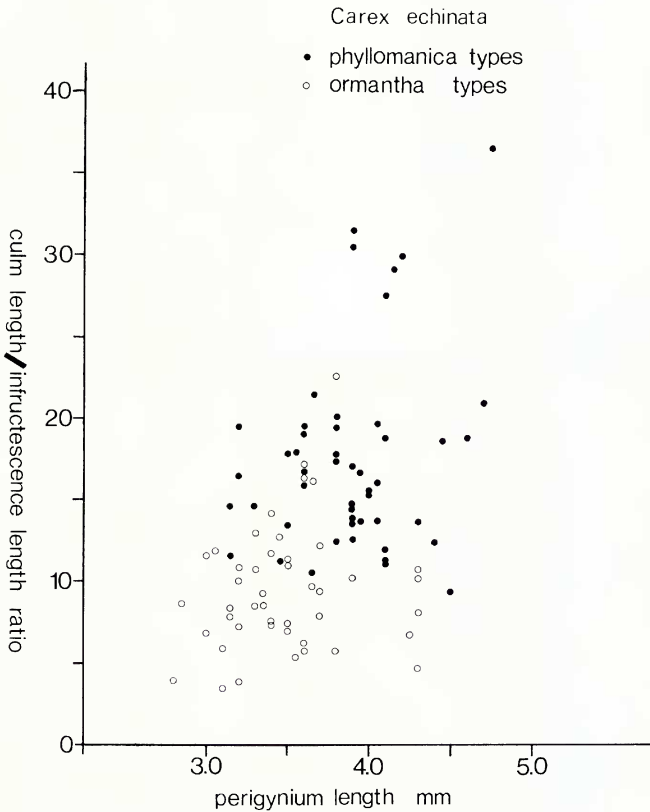


FIG. 12. Scatter plot of perigynium length and ratio of culm length to infructescence length for *Carex echinata* subsp. *phyllomanica* and "ormantha types."

C. laricina to 2.75 mm to 3.3 mm. Thus, it would seem that a frequency diagram of a wide selection of specimens of these plants should show few plants with perigynia 3.3 mm to 3.5 mm long. However, when such measurements are made on a large sample (Fig. 14) this is not the case. In fact, the sample formed a unimodal curve with a mean of 3.33 mm. The decisions of Fernald (1950) and Voss (1972) not to recognize *C. laricina* as distinct were clearly correct.

The problems are yet more involved, as up to now the two groups based on pistillate scale characters have been mostly discussed separately. As shown earlier, the features do not work reliably and, therefore, a cross-comparison of some of the species recognized by Mackenzie is in order. *Carex echinata* and *C. angustior* are both said to be nerveless on the adaxial surface but *C. echinata* should have ovate perigynia with short beak and *C. angustior* lanceolate perigynia with long beak. Figure 13, discussed earlier, shows that

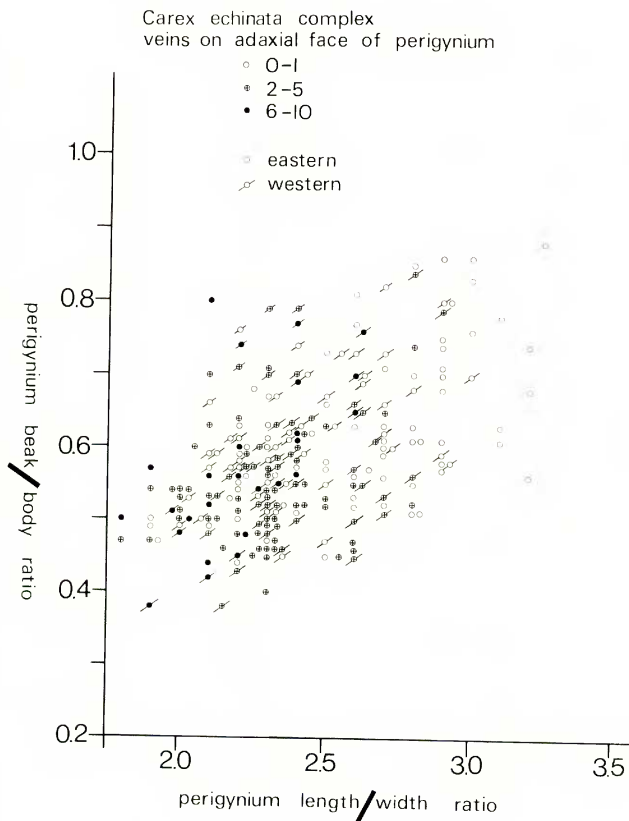


FIG. 13. Scatter plot of perigynium length/width ratio and perigynium beak length/perigynium body length ratio for *Carex echinata*.

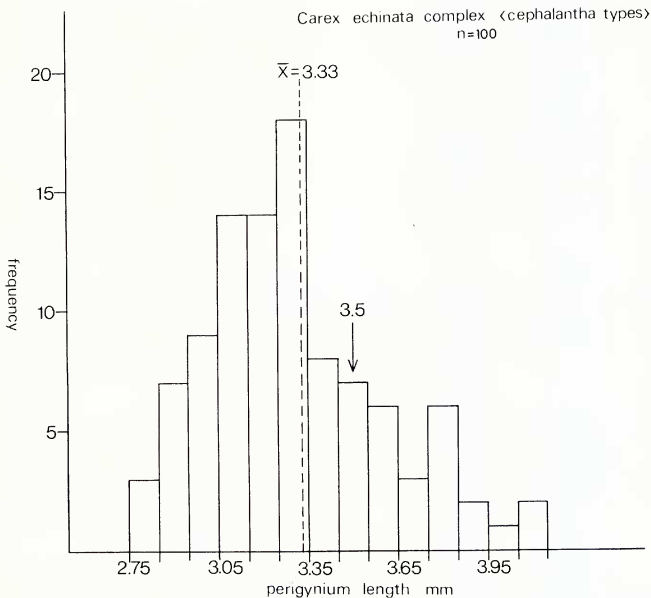


FIG. 14. Frequency diagram of perigynium length for *Carex echinata* "cephalantha types."

nerveless perigynia occur over a wide range of perigynium length/width ratios and perigynium beak/body ratios. No discontinuities were evident.

The variability of plants in western North America is such that Mackenzie (1931) had to recognize *Carex cephalantha* in collections of western plants and indeed, plants fitting this description do occur frequently in some parts of the west coast. Also, as noted earlier, plants with the very loose infructescences and long clavate terminal spikes characteristic of *C. ormantha*, as circumscribed by Mackenzie (1922, 1931), occur in the east (Fernald, 1902). Mackenzie separated the western and eastern plants by the nature of the pistillate scales but the unreliability of this feature has already been noted.

As in the *Carex atlantica* complex, the demonstration of discontinuities at the specific level has not been possible. Again, like the *C. atlantica* complex, the situation is more difficult than merely reducing the entire complex to one undivided species. A close examination of the complex throughout its range revealed a great deal of geographically correlated variation, thought not always in characters used by Mackenzie (1931). Western plants, regardless of their perigynium shape and inflorescence form, tend to be broader leaved. There is much overlap and, in essence, only the coastal plants that have been called *C. phyllomanica* have consistently much broader leaves than the extremes of the east. These coastal plants form a striking variant in the extreme but they do intergrade with *C. echinata* in the west and, rarely, plants similar in form will be found in

other parts of the species range. These coastal plants, with usually large perigynia, dense heads and broad leaves are here recognized as a well marked subspecies, *C. echinata* subsp. *phyllomanica*.

In New England and to a lesser extent in adjacent areas and the northern Great Lakes region, there occurs a somewhat higher proportion of narrow-leaved plants than in other areas. Exact proportions of western plants are: leaves less than 1.6 mm wide 4%, 1.6 to 2.55 mm wide 68%, and leaves greater than 2.55 mm wide 28%. Respective figures for all eastern plants are 34%, 56% and 10% and for New England only 65%, 23%, 12%. It is notable also that, as in the *Carex atlantica* complex and the western plants of the *C. echinata* complex, the widest-leaved plants in the east tend to be found near the coast. There is no doubt that all species of *Stellulatae* except *C. interior*, *C. sterilis*, and *C. ruthii* reach their greatest abundance and largest size in coastal regions. The eastern plants with narrow leaves are interesting. The narrowest-leaved extremes are often plants with extremely narrow perigynia, ca. 3 times as long as wide, and essentially nerveless on the adaxial surface. These plants correspond to the extreme of Fig. 13 with very narrow, nerveless perigynia. They have been called *C. angustior* Mackenzie. Mackenzie considered *C. angustior* to be a smaller plant with a denser infructescence than other species he recognized in the *C. echinata* complex, but these characters do not correlate well. This lack of correlation was responsible, in fact, for the description of *C. angustior* var. *gracilentia* (Clausen and Wahl, 1939) as that name refers to plants with elongate infructescences but narrow perigynia. Figure 13 also shows that these plants merely form a rare extreme of *C. echinata* with otherwise no significant trends present in the characters presented.

When the situation is examined in more detail, further resolution becomes difficult. Figure 15 shows the relationship of perigynium length/width ratio for samples from various portions of the range of *Carex echinata*. Figure 15A shows eastern *C. echinata* from the area where the plants with narrow perigynia tend to occur most frequently. It can be seen that the pattern is the same as in Fig. 13 with the plants with the narrowest perigynia being rare extremes. The length/width ratio is variable but no bimodality is evident. Figure 15B shows western North American plants referred by authors to *C. angustior*, *C. cephalantha*, and *C. echinata*. No extremes with very narrow perigynia are present in the sample examined. In Europe, perigynia ranged to approximately 2.8 times as long as wide in the limited sample examined. However, *C. angustior* has been reported for Asiatic U.S.S.R. (Egorova, 1960). The distribution of perigynium length/width ratio for the entire *C. echinata* complex in North America is shown in Fig. 15C. It can be seen that the pattern has changed little from Fig. 15A. The distribution is more or less skewed but with no clear-cut bimodality.

The feature of perigynium length/width ratio is one not equally expressed in all parts of the species' vast range. However, the extremes noted, although they mostly occur in northeastern North America, intergrade so completely that they cannot here be given formal taxonomic recognition. They are certainly not compatible with the morphogeographical subspecies recognized in this work. If it is desired to draw attention to this variant, the name *Carex echinata* Murray var. *angustata* (Carey) L. H. Bailey is available.

When western North American plants referred by Mackenzie and others to *Carex ormantha* were examined in detail, it was found that a higher proportion of plants with loose, long infructescences occurred in the Sierra Nevada of California than in other areas. However, as noted earlier, plants of the *C. echinata* complex with loose infructescences also occur in the east. No other characters were seen that correlated closely with the infructescence type. Like perigynium length/width ratio and leaf width, infructescence density is a feature whose expression is not equal throughout the range of the species. The lack of correlation of other features with infructescence type in plants with a lax infructescence and the lack of a precise geographical segregation of this variant make recognition of these plants as a separate taxon impossible. Again, if it

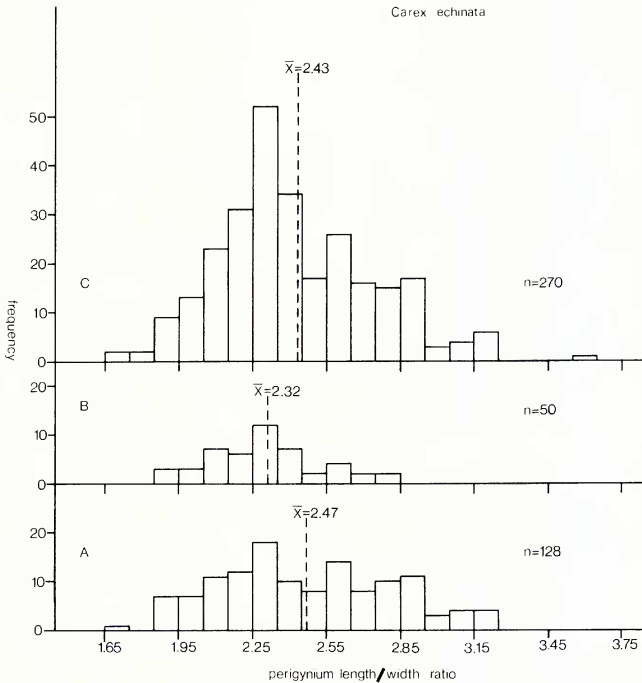


FIG. 15. Frequency diagram of perigynium length/width ratio for *Carex echinata* subsp. *echinata*, (A) selected specimens from Maine, Vermont, New Hampshire, Nova Scotia, Newfoundland, Quebec, New Brunswick, northern and central Ontario, northern New York, upper peninsula of Michigan, northern Wisconsin and northern Minnesota, (B) selected specimens from western North America, (C) selected specimens from throughout the North American range of the species.

is desired to draw attention to this variant, the name *C. echinata* Murray var. *ormantha* Fernald is available.

The Identity of North American and European *Carex echinata*

The relationship of North American plants to European plants has been often disputed. Most authors have been forced to admit this European species to the North American flora although its occurrence is often relegated to a restricted area. Mackenzie (1931) recognized it from only two areas of North America: in the east from Labrador, Newfoundland, and the Mingan Islands, Quebec, and in the west from Alberta and Alaska. However, Alberta specimens named *C. echinata* by Mackenzie are *C. interior*.

A summary of distinctions from all other North American species of the *Carex echinata* complex recognized by Mackenzie (1931) indicated *C. echinata sensu stricto* as having ovate, short-beaked perigynia, nerveless on the adaxial surface with obtuse or obtusish pistillate scales. In his description, Mackenzie notes the perigynia as being 2.5 to 3.0 mm long and 1.2 to 1.8 mm wide. His description also calls for a plant 15 to 35 cm high with 2 to 3 spikes and leaves 1.0 to 2.0 mm wide (Table 1).

When a selection of 56 specimens representing a wide geographical range from Spain and the Azores to Scandinavia and Russia was examined for these and other features, the results were quite interesting. The absolute range of perigynium length was 2.65 to 4.3 mm and the mean of the sample was 3.42 mm. This mean is well beyond the maximum size given for *Carex echinata* perigynia by Mackenzie (1931). Perigynium width ranged from 1.2 to 2.05 mm. The length/width ratio ranged from 1.75 to 2.8. The number of spikes ranged up to 5 and leaf width up to 2.8 mm even in the limited sample examined. Plants examined ranged to over 40 cm tall and, although no fully elongated fruiting specimens were seen, some had broken culms of the previous year that indicated that they were quite tall when fully grown. Division of the lower pistillate scales into acute and obtuse classes disclosed that, of 55 specimens, 34 had acute and 21 obtuse scales. The pistillate scale apex is also described and pictured as acute in Jermy and Tutin (1968). Accurate comparison with Mackenzie's description is made rather difficult by his use of the term "obtusish."

Table 1: Comparison of measurements from 56 European *Carex echinata* with values given for North American *C. echinata* by Mackenzie (1931) for specific characters.

Character	Mackenzie (1931)	European <i>C. echinata</i>
Culm length	15–35 cm	10–42 cm (maximum value not observed)
Widest leaf	2.0 mm	2.8 mm
No. spikes	2–3	2–5
Perigynium length	2.5–3.0 mm	2.65–4.3 mm
Perigynium width	1.2–1.8 mm	1.2–2.05 mm

Plants with perigynia both nerved and not nerved on the adaxial surface are found in Europe. From a sample of 56 plants, 21 had 2–6 veins on the adaxial surface and 35 had 1 vein or none. As well, there is great variability in beak length and the portion of the body below the beak that is serrulate-margined. Infructescence density is also quite variable. In Europe as in North America, it may range from loose with widely spaced spikes to dense infructescences reminiscent of *C. echinata* subsp. *phyllomanica* of the west coast of North America. *Carex echinata* in Europe is quite variable, just as it is in North America.

It is evident from the previous discussion that if Mackenzie's (1931) delimitations of species are used objectively on European specimens, then surely almost all North American taxa of the *Carex echinata* complex recognized by Mackenzie would also have to be recognized in Europe. Mackenzie's description of *C. echinata* does not fit the common "Star Sedge" of Europe. Even on the basis of the limited sample of European *C. echinata* examined, the plant is much more variable than allowed by Mackenzie for North American *C. echinata*. Mackenzie's delimitation of the species was much too narrow. It is likely that Mackenzie felt that the European species should occur in North America only at high latitudes and altitudes and in subarctic habitats. The opinion that only arctic and subarctic species were likely to be common to Europe and North America was also held by Bailey (1893). Mackenzie may well have based his description and delimitation of the species on these dwarfed plants, without taking into account the variation found in Europe. The recognition of different species in North America has been shown to be untenable. Also, although there is little doubt that the species is more

variable in North America, much of the variability shown by North American plants can be found in European plants, as pointed out long ago by Fernald (1902).

Löve (1954a, b) has argued that the European *Carex echinata*, *C. cephalantha*, and *C. angustior* are distinct species because they differ in chromosome number. The European plants are reported to have a chromosome number of $2n = 58$ whereas *C. angustior* and *C. cephalantha* have had counts noted of $2n = 50$ and $2n = 52$ respectively. No morphological discussion in support of this was presented. The blanket statement that they must be different species if their chromosome numbers (here determined on a very limited sample) are different is unacceptable in *Carex*. The various problems hampering the free use of chromosome data in *Carex* have been discussed previously (Moore and Calder, 1964; Faulkner, 1972; Reznicek, 1978).

Carex echinata of Europe and Asia and the *C. echinata* complex in North America are here viewed as a single, variable species. This places it with other variable circum-boreal species such as *C. curta* Good., (*C. canescens* auct. non L.), *C. diandra* Shrank, *C. brunnescens* (Pers.) Poir., *C. aquatilis* Wahl., *C. magellanica* Lam., *C. livida* (Wahl.) Willd., *C. vaginata* Tausch, *C. capillaris* L., and *C. rostrata* Stokes. Some of these species, such as *C. curta*, *C. diandra*, and *C. magellanica*, are also, like *C. echinata*, found in the temperate parts of the southern hemisphere.

Comments on Taxonomic difficulties in the *Stellulatae*

Both in the *Carex atlantica* complex and the *C. echinata* complex other characters were examined and had the same basic geographical trends of variation as the examples discussed above. No other patterns that could be resolved into morphogeographical variants susceptible of recognition in a formal taxonomic hierarchy could be discerned.

The basic problems with the present taxonomy of the *Stellulatae*, especially the *Carex atlantica* and *C. echinata* complexes, were the arbitrary division of continuous series of variation in certain characters into artificial taxa, and, concomitant with this, a much too narrow circumscription of taxa. Specific limits were occasionally placed in such a manner that they fell near the mode of the variation in certain characters. It is no wonder that this group has gained notoriety as an extremely difficult area of the genus *Carex*. The after-effects of such problematical taxonomy are not desirable.

First, the group gains a perhaps unwarranted reputation for being difficult and thus taxonomists working on a flora are unlikely to deal adequately with it. Also, if taxonomists examine their plants closely and find that in their area they do not compare accurately with published species descriptions, they are liable, if a complete revision of the group is not undertaken, to describe new varieties *ad infinitum* to account for variation that should have been included with the description of the species in the first place. This phenomenon has been noted for other critical groups (Davis and Heywood, 1963) and such may have been the case with *C. interior* subsp. *charlestonensis* Clokey (1939), *C. interior* var. *keweenawensis* Hermann (1941), *C. angustior* var. *gracilentata* Clausen and Wahl (1939), and *C. sterilis* var. *rousseauiana* Raymond (1950). As well, more or less intermediate plants may be considered hybrids, as is evident from annotations on herbarium specimens. Lastly, taxonomists may examine the variation of alleged species based on specimens in herbaria, throw up their hands in frustration, and place everything into one species. None of these alternatives is desirable.

TAXONOMIC TREATMENT

Carex L. section *Stellulatae* Kunth, Enum. Pl. 2: 399. 1837.

Rhizomes short; plants cespitose; roots pale yellow to dark brown, smooth. Culms aphyllopodic with persistent basal sheaths; leaves all in basal third, usually plicate to flat, upper blades usually larger than lower; sheaths covering nodes, usually glabrous. Spikes

usually gynecandrous; pistillate scales ovate, obtuse to acute, one-veined, usually yellow to castaneous with green center and hyaline margins, staminate scales lanceolate to ovate, usually acute, usually yellow to castaneous with green center and hyaline margins. Lower perigynia of spikes spreading to usually reflexed at maturity, lanceolate to suborbicular, tapering to a beak, plano-convex to slightly biconvex, sessile, spongy-thickened at base surrounding achene, nerveless or several-nerved adaxially, usually several- to many-nerved abaxially; beak usually serrulate on margin and toothed apically; achenes usually ovate to suborbicular, biconvex, sessile; style deciduous; stigmas 2; anthers 3..

The *Stellulatae* are very widespread in North America. At least one species is found in every province and territory of Canada and all states of the United States except, as yet, Oklahoma. Southward, it is found through Mexico and Guatemala. World-wide, the section is known from Europe, north-eastern Asia to Japan, New Zealand, Australia, New Guinea, and Sumatra. However, the greatest diversity of species is in North America, especially in eastern regions.

Although occurring in a wide range of habitats the *Stellulatae* nevertheless exhibit a number of common preferences. They are all species of open wetlands, only occasionally ranging into wet forests. Quite frequently, they occur in bogs, fens, and wet meadows but much less commonly in taller wetland vegetation such as *Typha* or *Scirpus* marshes or shrub carrs.

The section is very difficult taxonomically in North America and most species can overlap slightly with each other in all characters although, of course, all characters never overlap on any one plant. Identification is, therefore, quite difficult. In using the key, dimensions must be carefully measured and the best fitting lead of the couplet selected after examination of all characters given. In case of doubt, identifications should always be confirmed by comparison with authentically determined herbarium material.

KEY TO STELLULATE OF NORTH AMERICA

- | | |
|--|---|
| 1. Spikes usually solitary; leaves involute; anthers 2.0–3.6 mm. | 1. <i>C. exilis</i> |
| 1. Spikes 2–8; leaves flat or plicate; anthers 0.6–2.2 (2.35) mm. | 2. |
| 2. Perigynium beak smooth-margined. | 8. <i>C. seorsa</i> |
| 2. Perigynium beak at least sparsely serrulate on margins. | 3. |
| 3. Widest leaves 2.8–5.0 mm wide. | 4. |
| 3. Widest leaves 0.8–2.7 mm wide. | 7. |
| 4. Lower perigynia of spikes mostly 1.1–1.6 times as long as wide, mostly 2.1–3.0 mm wide. | |
| | 6a. <i>C. atlantica</i> subsp. <i>atlantica</i> |
| 4. Lower perigynia of spikes (1.5) 1.7–3.0 times as long as wide, mostly 1.2–2.0 mm wide. | 5. |
| 5. Longer pistillate scales 2.1–3.1 mm long; west coast of North America. | |
| | 7b. <i>C. echinata</i> subsp. <i>phyllomanica</i> |
| 5. Longer pistillate scales 1.4–2.2 mm long; eastern North America. | 6. |
| 6. Infructescences mostly 15–30 mm long, lowest 2 spikes 1.3–9.5 mm distant. | 4. <i>C. wiegandii</i> |
| 6. Infructescences mostly 30–85 mm long, lowest 2 spikes 10–40 mm distant. | 5. <i>C. ruthii</i> |
| 7. Terminal spikes entirely staminate; anthers (1.0) 1.2–2.2 (2.35) mm long. | 2. <i>C. sterilis</i> |
| 7. Terminal spikes partly or wholly pistillate; anthers 0.6–2.2 (2.35) mm long. | 8. |
| 8. Terminal spikes without a distinct clavate base of staminate scales, staminate portion less than 1 mm in length; anthers (1.0) 1.2–2.2 (2.35) mm long. | 2. <i>C. sterilis</i> |
| 8. Terminal spikes with a distinct clavate base 1.0–16.5 mm long of staminate scales; anthers 0.6–1.6 (2.0) mm long. | 9. |
| 9. Lower perigynia 2.0–3.0 mm wide. | 6a. <i>C. atlantica</i> subsp. <i>atlantica</i> |
| 9. Lower perigynia 0.9–1.95 mm wide. | 10. |
| 10. Lower perigynia mostly 1.9–3.0 mm long, 1.0–2.0 (2.2) times as long as wide; beaks mostly 0.4–0.95 mm long, mostly 0.2–0.5 times as long as body. | 11. |
| 10. Lower perigynia mostly 2.85–4.75 mm long, (1.7) 1.8–3.6 times as long as wide; beaks mostly 0.95–2.0 mm long, mostly 0.45–0.85 times as long as body. | 13. |
| 11. Perigynia mostly nerveless over achene on adaxial surface; beak of perigynium conspicuously setulose-serrulate; perigynia often more or less convexly tapered from widest point to beak, forming a "shoulder." | 3. <i>C. interior</i> |

11. Perigynia mostly 1–10-nerved over achene on adaxial surface; beak of perigynium more sparsely serrulate with definite spaces between the often single teeth; perigynia mostly more or less cuneate or even concavely tapered from widest point to beak. 12.
12. Widest leaves 1.6–2.7 mm wide, infructescence mostly 18–45 mm long.
6a. *C. atlantica* subsp. *atlantica*
12. Widest leaves (0.65) 0.8–1.6 mm wide, infructescence mostly 8–20 mm long.
6b. *C. atlantica* subsp. *capillacea*
13. Heads very dense, 12–25 (40) mm long; distance between lower 2 spikes usually less than length of lowest spike. 14.
13. Heads more lax, usually 25–80 mm long; distance between lower 2 spikes usually more than length of lowest spike.
7a. *C. echinata* subsp. *echinata*
14. Perigynia 2.85–3.6 (4.0) mm long, often nerveless over achene on adaxial surface; widest leaves 1.0–2.4 (2.7) mm wide; widespread.
7a. *C. echinata* subsp. *echinata*
14. Perigynia (3.1) 3.5–4.75 mm long, usually 2–12-nerved over achene on adaxial surface; widest leaves (1.7) 2.3–2.7 mm wide; west coast of North America.
7b. *C. echinata* subsp. *phyllomanica*

1. *Carex exilis* Dewey, Am. Jour. Sci. Arts 14: 351. 1828. Holotype in herb. Dewey: Danvers [Massachusetts], Oakes, GH(!). Isotypes GH(!) NY(!) WIS(!).

C. exilis var. *squamacea* Dewey, Am. Jour. Sci. Arts 14: 351. 1828. Holotype in herb. Dewey: Ipswich, Mass., Oakes, GH(!). Isotypes PH (2 sheets) (!), NY (2 sheets) (!), WIS (2 sheets) (!).

C. exilis var. *androgyna* Dewey in Wood, Class Book of Botany: 750. 1861. Probable isotype: Manchester, Essex Co., N. Y. P. D. K[nieskern]. GH(!).

Rhizomes short; plants densely caespitose; roots smooth, pale yellow to dark grey-brown; culms 12–80 cm, erect, elongating in fruit, phyllopodic, obtusely trigonous, smooth; basal sheaths persistent, dark brown. Leaves 2–6 per culm, all in basal third, usually shorter than culms in fruit; blades 4–70 cm × 0.4–1.5 mm in diameter, involute, smooth or antrorsely scabrous; lower blades of culms often longer than upper and blades of sterile shoots longer; widest leaf 0.8–1.5 mm in diameter. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 3.5–21 cm; inner band hyaline, not purple-dotted; sheath apex concave, scarcely thickened; ligule 0.8–1.8 mm × 0.6–1.6 mm, rounded. Infructescence 6–40 mm; spike solitary (occasionally 1 or 2 (3) smaller accessory spikes below main one), pistillate above and staminate below or plants sometimes dioecious. Pistillate portion of spike 5.0–9.5 mm wide, up to 27-flowered; staminate portion of spike 1.0–3.0 mm wide, up to 50-flowered. Pistillate scales 1.8–3.3 mm × 1.3–2.2 mm, ovate, one-veined, acute, castaneous with green center and hyaline margins. Staminate scales 1.7–5.5 mm × 1.0–2.2 mm, lanceolate to ovate, one-veined, acute, castaneous with green center and hyaline margins. Lower perigynia of spikes spreading to reflexed, lanceolate-ovate to very broadly ovate, 2.6–4.7 mm × 1.25–2.3 mm, 1.3–2.65 times as long as wide; tapering to a beak, plano-convex or slightly biconvex, castaneous when first ripe, dark brown when over-mature; more or less sessile, spongy-thickened at base surrounding achene; adaxial veins up to 7, faint; abaxial veins up to 15, faint; serrulate on margins up to 1.2 mm below base of beak. Beak 0.5–1.7 mm, 0.2–0.65 times as long as body; serrulate on margins, toothed apically; teeth blunt, soft, sometimes obsolete or up to 0.35 mm. Achenes 1.4–2.2 mm × 1.2–1.7 mm, ovate, biconvex; style deciduous, stigmas 2. Anthers 3, (2.0) 2.2–3.6 mm. Fig. 26 (perigynia) and 36 (infructescences).

This very distinctive member of the *Stellulatae* is notable for its striking, large, single spikes. It was described early and its nomenclature and typification present no problems.

Although very distinct from all other *Stellulatae*, perigynium shape and size in this species are quite variable as shown in Fig. 26. The perigynia range from very narrowly ovate to very broadly ovate and beak length is exceedingly variable as well. Plants with accessory spikes below the main one may resemble other species of *Stellulatae* but are

separable by their involute leaves, large anthers, and the fact that the terminal spike is much larger than the laterals. Other *Stellulatae* may have the terminal spike slightly larger than the laterals but not strikingly so. These multiple-spiked plants, when growing with both single-spiked *Carex exilis* and other species of *Stellulatae*, are likely responsible for reports of hybrids (Mackenzie, 1931; Raymond, 1952; Moore and Calder, 1964) as discussed by Marie-Victorin and Rolland-Germain (1969).

The position of *Carex exilis* in the *Stellulatae* is quite isolated. Boott (1858) felt that it was allied with *C. sterilis*. This is plausible as the species do share certain features such as large anthers, a more densely cespitose habit than most other *Stellulatae*, and a tendency to be more or less dioecious. In any case, it appears that the plant is not close to members of the *Dioicae* group as has been proposed by Tuckerman (1843), Kükenthal (1909), Savile and Calder (1953), and Toivonen and Timonen (1976).

The distribution of the species is quite interesting (Fig. 16). From Delaware northwards to Massachusetts it is continuous along the coast. From there it occurs inland through New York to western Ontario and Minnesota and north along the coast to central Labrador. Southwards from Delaware, it is known from two isolated localities, one in Moore County, North Carolina, (record from Radford, Ahles, and Bell, 1964) and one from George County, Mississippi (At Miss.-Ala. line; off Hwy 98 about 200–300 yds.

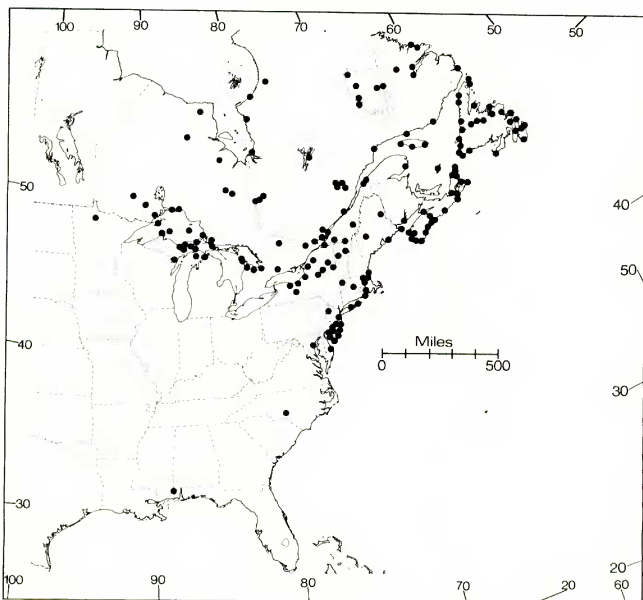


FIG. 16. Distribution of *Carex exilis*.

to right (south) of Hwy. Ken E. Rogers 2919, April 12, 1970, NCU). These southern records are likely relicts of a former wider distribution in the wetlands of the southern coastal plain during the glacial maxima. The species found the vast bogs and fens of newly deglaciated territory a very suitable habitat and spread widely from the area where glaciated territory touched the coastal plain as in New Jersey and Long Island, New York. *Carex exilis* is probably still in the process of migration northwards and westwards. Such a pattern is also shown by *Sarracenia purpurea*, a frequent associate of *C. exilis* in bogs and fens (Gleason and Cronquist, 1964).

The ecology of *Carex exilis* is quite restricted. It grows in extreme fens and bogs and, like *Sarracenia purpurea* mentioned above, with little regard for calcareous or acidic habitats but always in open, wet sites of low cover.

2. *Carex sterilis* Willdenow, Sp. Pl. 4: 208. 1805. Holotype in herb. Willdenow: No. 17109b "Pennsylvania, Muhlenberg." B, photo TRTE(!). Probable isotypes GH(!), PH (3 sheets) (!).

C. stellulata Gooden. var. *sterilis* (Willd.) Carey, Carices N. U.S. 554. 1847.

C. elachycarpa Fernald, Proc. Am. Acad. Arts Sci. 37: 492. 1902. Holotype: Fort Fairfield, Valley of Aroostook River, Aroostook Co., Maine. Mabel P. Cook, Elsie L. Shaw, M. L. Fernald, June 29, 1899. GH(!). Isotypes GH(!), NEBC(!).

Kobresia elachycarpa (Fern.) Fernald, Rhodora 5: 251. 1903.

C. sterilis Willd. var. *rousseauiana* Raymond, Nat. Can. 77: 62. 1950. Holotype: Anticosti, Rivière Chicotte: berge graveleuse à l'embouchure. 17 juillet 1942. Rousseau 52 333 MT(!). Isotypes MTJB(!), MICH(!).

C. Xminganinsularum Raymond, Bull. Soc. Bot. France 99: 197. 1952. Lectotype (*des. nobis*): Québec: [comité de Saguenay]. Archipel de Mingan: île à la Proie, Marie-Victorin, Rolland-Germain et Louis-Marie 20.116, 22 juillet 1925. MT(!). Isolectotype MT(!).

C. muricata L. var. *sterilis* (Willd.) Gleason, Phytologia 4: 22. 1952.

Rhizomes short; plants caespitose, often densely so; roots smooth, pale yellowish to brown; culms 10–75 cm, erect, elongating in fruit, aphyllipodic, scabrous on angles above; basal sheaths persistent, brownish. Leaves 3–5 per culm, all in basal third, shorter than culms in fruit; blades 7.5–25 cm × 1.2–2.6 mm, plicate, antrorsely scabrous above; upper blades of culm much longer than lower and blades of sterile shoots longer; widest leaf 1.6–2.6 mm wide. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 4.0–13 cm; inner band hyaline; sheath apex concave, scarcely thickened; ligule 0.3–1.7 mm, rounded to obtuse. Infructescence 0.9–4.0 cm, densely crowded above but often with the lower spikes more or less separate; spikes 3–8. Plants more or less dioecious; pistillate plants with rarely a few staminate flowers; predominately staminate plants sometimes with a few pistillate flowers scattered on the spikes or occasionally entirely pistillate spikes mixed with entirely staminate ones in the same infructescence. Terminal spikes 3.5–13.7 mm, usually unisexual, 4.5–7.2 mm wide and 5–26-flowered when pistillate, 1.2–2.6 mm wide and 6–31-flowered when staminate. Lateral spikes 3.0–13.5 mm, similar to terminal spikes. Distance between upper 2 spikes 0.3–1.5 (5) mm; distance between lower 2 spikes 3.8–15.5 mm; lateral spikes with short, scale-like bracts. Pistillate scales 1.8–2.9 mm × 1.0–1.8 mm, ovate, one-veined, acute, castaneous with green center and usually conspicuous, broad hyaline margins. Staminate scales 2.2–3.3 mm × 1.1–1.8 mm, ovate, one-veined, acute, castaneous with green center and broad hyaline margins. Lower perigynia of spikes spreading to reflexed, ovate to deltoid, 2.1–3.8 mm × 1.2–2.2 mm × 1.4–2.3 (2.7) times as long as wide, tapering to a beak, plano-convex, castaneous when first ripe, almost black when over-mature, sessile, spongy-thickened at base surrounding achene; adaxial veins absent or up to 10; abaxial veins 5–12; strongly setulose-serrulate on margins to 0.2–0.8 mm below base of beak. Beak 0.65–1.6 mm, 0.45–0.8 times as long as body, copiously setulose-serrulate on margins, toothed apically; teeth soft, often flexuous, whitish, 0.15–0.5 mm. Achenes 1.0–1.7 mm

X 0.9–1.3 mm; ovate to suborbicular, biconvex, sessile; styles deciduous; stigmas 2. Anthers 3, (1.0) 1.2–2.2 (2.35) mm. Figs. 27 (perigynia) and 37 (infructescences).

In its tendency to a dioecious habit, *Carex sterilis* is very unusual among plurispicate *Carex*. It was the first exclusively North American species to be described and its nomenclature and typification are straightforward. Fernald's (1902) use of the name for what is now called *C. atlantica* was clearly an error, as pointed out by Mackenzie (1910). Willdenow's type is dioecious as both male and female spikes are clearly visible on the sheet.

Carex sterilis presents an unusual array of infructescence types. All-male plants are intermingled with all-female plants and occasional intermediate forms. In the very rare instance of an individual of *C. sterilis* having a more or less gynecandrous terminal spike, close examination is necessary to place it. The most reliable feature is the long anthers of the plant, up to 2.2 (2.35) mm. This is longer than any species except the distinctive *C. exilis*. *Carex sterilis* also has more prominent castaneous and hyaline margins to the pistillate scales, a more densely setulose-serrulate margin to the beak, and less stiff, often more hyaline apical teeth on the beak than is usual for most individuals of other species. These features are of particular assistance when comparative material is available.

Carex sterilis does not have any very close relatives in the *Stellulatae*. It is similar to *C. interior* in its blunt scales with broad hyaline margins and its densely setulose-serrulate perigynium beak, but *C. interior* has small anthers, a gynecandrous terminal spike, and a beak less than 0.45 times as long as the perigynium body. The similarity of *C. sterilis* to *C. exilis* in some respects has already been discussed under the latter species.

As noted before, most species of *Stellulatae* tend to be coastal (or montane) but *Carex sterilis* is primarily a plant of the interior. Its range is divided into two parts (Fig. 17). The major portion centers on the Great Lakes region. In certain areas here the plant is quite common in its habitat. Outlying areas occur in Minnesota, Manitoba, and Saskatchewan; the central part of northern Ontario, north to James Bay; and, in the east, to eastern Pennsylvania, eastern New York, and rarely to extreme western Connecticut and

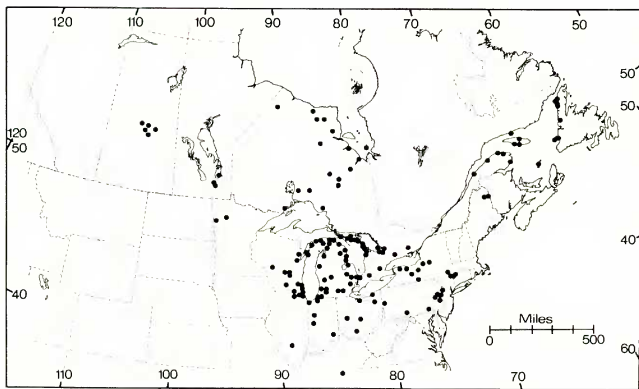


FIG. 17. Distribution of *Carex sterilis*.

Massachusetts. There is then a large gap in the species range until the region of the Gulf of St. Lawrence. There, the species occurs sparingly from the Aroostock River Valley of northern Maine to the Mingan Islands, Quebec, and east to western Newfoundland. It is a calciphile and the gap is likely due to a scarcity of suitable habitats. No significant differences were noted between plants from the Gulf of St. Lawrence and the Great Lakes region. Reports of *C. sterilis* in older literature from other parts of North America are due to past misuse of the name for *C. atlantica* or *C. echinata*. *Carex sterilis* has virtually its entire range in newly glaciated territory and presumably survived glaciation in suitable habitats just south of the glacial front.

The preferred habitat of this species is quite restricted. It is an obligate calciphile occurring in fens, marl meadows, calcareous lake and river shores, moist limestone flats, wet prairie, and open, calcareous Cedar and Tamarack swamps. The habitat of the plant is of considerable help in identification as most other *Stellulatae* except *C. interior* and *C. exilis* prefer acidic sites. In its favoured habitat, the plant may be abundant, sometimes dominating small areas. Its stiff culms in dense clumps are a distinctive feature of many fens, marly meadows, and calcareous shores.

3. *Carex interior* L. H. Bailey, Bull. Torr. Bot. Club 20: 426. 1893. Lectotype (*des. nobis*): Penn Yan, New York, No. 36, H. P. Sartwell, Carices Americae Septentrionalis Exsiccatae, Pars 1, 1848. GH(!). Isolectotypes NY(!), PH(!).

C. scirpoides Willdenow, Sp. Pl. 4: 237. 1805. *Non C. scirpoidea* Michaux, Fl. Bor. Am. 2: 171. 1803.

C. stellulata Gooden. var. *scirpoides* (Willd.) Darlington, Fl. Cestrica 31. 1837.

C. stellulata Gooden. var. *scirpina* Tuckerman, Enumeratio Methodica Caricum Quarundam. 9. 1843. *Nom. illeg.* Based on *C. scirpoides* Willd.

C. sterilis Willd. forma *flexibilis* Farwell, Ann. Rep. Mich. Acad. Sci. 21: 362. 1920. Holotype: Lakeville [Oakland Co., Michigan]. O. A. F[arwell] 4887, June 2, 1918. BLH n.v. Isotype MICH(!).

C. interior L. H. Bailey subsp. *charlestonensis* Clokey, Bull. S. Calif. Acad. Sci. 38: 1. 1939. Holotype: Charleston Park, Charleston Mts., Clark Co. Nevada. I. W. Clokey 7468, June 19, 1937. UC(!). Isotypes GH(!), PH(!), TEX(!), UC(!), MICH(!), CM(!).

C. interior L. H. Bailey var. *keweenawensis* F. J. Hermann, Am. Midl. Nat. 25: 19. 1941. Holotype: Southeast of Eagle Harbor, Keweenaw Co. Michigan, F. J. Hermann 7985, July 13, 1936. GH(!). Isotypes PH(!), MICH(!).

C. interior L. H. Bailey forma *keweenawensis* (F. J. Hermann) Fernald, Rhodora 44: 284. 1942.

Rhizomes short; plants caespitose; roots smooth, yellowish to dark brown; culms 10–95 cm, erect, elongating in fruit, aphyllopodic, smooth; basal sheaths persistent, light brown. Leaves 3–5 per culm, all in basal third, often shorter than culms in fruit; blades 6–31 cm × 0.6–2.4 (2.7) mm, plicate, antrorsely scabrous on margins above; upper blades of culm longer than lower and blades of sterile shoots longer; widest leaf 1.0–2.4 (2.7) mm. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 1.8–13.0 cm; inner band hyaline, sometimes purple dotted; sheath apex concave, not or scarcely thickened; ligule of uppermost culm leaf 0.6–2.2 mm, obtuse to rounded. Inflorescence 8–37 mm, dense to more or less lax; spikes 2–5 (6). Terminal spike 5.2–20 mm, staminate at base, pistillate above; staminate portion 2.2–14.5 mm × 0.7–1.4 mm, 3–10-flowered; pistillate portion 3.0–7.0 mm × 4.0–5.8 mm, 4–16-flowered. Lateral spikes 3.0–9.5 mm, sessile, pistillate with often a few staminate flowers at base; staminate portion up to 2.2 mm and 3-flowered; pistillate portion 2.3–8.0 mm, 3–18-flowered. Distance between upper 2 spikes 0.4–5.8 mm, distance between lower 2 spikes 2.1–11.0 mm; lateral spikes with short scale-like bracts. Pistillate scales 1.2–2.1 (2.4) × 1.0–1.6 mm, ovate, one-veined, usually obtuse, castaneous with green center and broad hyaline margins. Staminate scales 1.4–2.9 mm × 1.0–1.3 mm, ovate, one-nerved, obtuse to acute, castaneous with green center and hyaline margins. Lower perigynia of spikes spreading to reflexed, ovate to broadly ovate, 1.95–3.0 (3.3) mm × 1.1–1.8 mm, 1.4–2.0 (2.2) times as long as wide; tapering to a beak, plano-convex to slightly biconvex,

green to mostly castaneous when first ripe, dark brown when over-mature, sessile, spongy-thickened at base surrounding achene, serrulate on margins up to 1.0 mm below base of beak; adaxial veins over achene none or occasionally up to 6; abaxial veins 4–12, sometimes faint. Beak 0.4–0.95 mm, 0.18–0.44 times as long as body, setulose-serrulate on margins, apex toothed; teeth more or less blunt, 0.15–0.4 mm. Achenes 1.2–1.8 mm X 0.95–1.5 mm, ovate, biconvex, sessile; style deciduous; stigmas 2. Anthers 3, 0.6–1.4 mm. Figs. 28 (perigynia) and 38 (infructescences).

Over much of North America, especially the central parts, this small species is the commonest or only representative of the *Stellulatae*. The plant was long known as *Carex scirpoides* Willd. However, since that name differs only in the last letter of the Latin termination from the earlier *C. scirpoidea* Michaux, it is here regarded as a later homonym. Bailey's name was the next available for the taxon at the specific level and is in common use in all floristic and taxonomic works at the present time.

For such a wide-ranging taxon, the uniformity of *Carex interior* over its range is surprising. Virtually no attempts have been made to segregate the species into several taxa except for the description of the form with perigynia nerved on the adaxial surface as both *C. interior* subsp. *charlestonensis* and *C. interior* var. *keweenawensis*. The nerved form, although occurring sporadically throughout the range of *C. interior*, is apparently more frequent than the nerveless form in the Rocky Mountain states (Hermann, 1970).

Rarely, specimens were seen that were intermediate in beak length, perigynium length and perigynium shape between *Carex interior* and *C. echinata*. These plants may represent hybrids although they appear fertile on superficial examination. These plants were often similar to the description of *C. laricina*. Interestingly enough, although this species has been aligned with *C. atlantica* subsp. *capillacea* in the past, no intermediates were noted in this study.

Carex interior, with its wide distribution in the southwestern United States and Mexico as well as across the continent farther north, is not a recently evolved species (by *Stellulatae* standards). Over wide areas of its range, it is not now sympatric with other species of *Stellulatae*. Its nearest relatives in the *Stellulatae* are *C. echinata*, noted above, and also, more interestingly, the broad-leaved *C. wiegandii*, a rare species of northeastern North America. The small anthers and short, usually obtuse pistillate scales of *C. wiegandii* are similar to those of *C. interior* and, although *C. wiegandii* is a larger plant, there is much overlap in perigynium length, beak length, and perigynium length/width ratio. The distant similarity of *C. interior* to *C. sterilis* has already been noted.

The distribution of *Carex interior* is shown in Fig. 18. Additional Mexican localities are noted in Hermann (1974). The species is reported, undoubtedly correctly, from New Mexico as well (Wootton and Standley, 1915). In the east, the plant has been reported from West Virginia (Core, 1938) and Virginia (Harvill, 1973). As it occurs in adjacent southern Pennsylvania, the species may well occur in these states, but all specimens examined have been either *C. atlantica* or *C. echinata*.

The preferred habitats of *Carex interior* are calcareous, although it is not so specific as *C. sterilis* in this regard. It never grows in acidic *Sphagnum* bogs or similar sites but is found in a wide variety of lake, river, and stream shores, ditches, sedge meadows, wet prairies, fens, Cedar, Tamarack, and Spruce swamps and, occasionally, wet mixed woods.

4. *Carex wiegandii* Mackenzie, N. Am. Fl. 18: 108. 1931. Lectotype (*des. nobis*): Silurian hills back of Birchy Cove (Curling), Region of Humber Arm, Bay of Islands, Western Newfoundland, M. L. Fernald and K. M. Wiegand 2776, July 21, 1910. GH(!). Isolectotype F(!).

Rhizomes short; plants caespitose; roots smooth, pale yellow-brown to dark grey-brown; culms 10–105 cm, erect, elongating in fruit, aphyllopodic, smooth to slightly scabrous above; basal sheaths persistent, brown. Leaves 3–8 per culm, all in basal third,

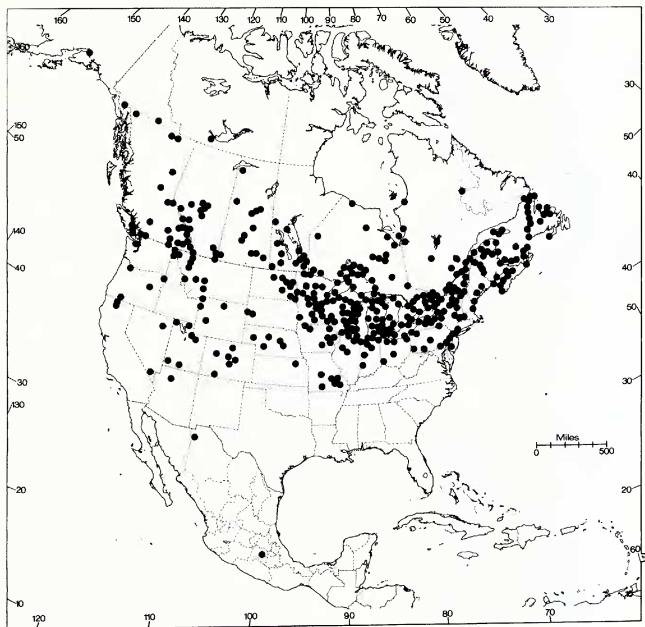


FIG. 18. Distribution of *Carex interior*.

usually shorter than culms in fruit; blades 11–45 cm \times 1.7–5.0 mm, plicate, antrorsely scabrous above, upper blades of culm much longer than lower and blades of sterile shoots longer; widest leaf 2.8–5.0 mm. Sheaths covering nodes, tight, glabrous or sometimes hispidulous on the veins, that of uppermost leaf 4–23 cm; inner band hyaline, rarely purple dotted; sheath apex concave, strongly thickened; ligule 0.9–2.5 mm, rounded to obtuse. Inflorescence 8.6–30 mm, dense; spikes 4–6. Terminal spike 6.1–14.5 mm, staminate at base, pistillate above; staminate portion 2–8.6 mm \times 0.8–1.3 mm, 5–20-flowered; pistillate portion 3.0–8.0 mm \times 5.0–7.3 mm, 7–25-flowered. Lateral spikes 4.5–8.0 mm, sessile, pistillate at apex and staminate at base; staminate portion (0) 0.5–2.0 mm, (0) 1–3-flowered; pistillate portion 3.0–8.0 mm, 5–21-flowered. Distance between upper 2 spikes 0.8–3.0 mm, distance between lower 2 spikes 1.3–9.5 mm; lateral spikes with short, scale-like bracts. Pistillate scales 1.45–2.0 (2.2) mm \times 1.3–1.9 mm, ovate, one-veined, obtuse to subacute, sometimes shortly mucronate, castaneous with green center and hyaline margins. Staminate scales 1.2–2.3 mm \times 1.4–1.8 mm, ovate, one-veined, obtuse to acute, castaneous with green center and hyaline margins. Lower perigynia of spikes spreading to reflexed, broadly ovate, 2.55–3.75 mm \times (1.25) 1.4–2.0 (2.1) mm, (1.4) 1.6–2.5 times as long as wide, tapering to a beak, plano-convex, green to castaneous when first ripe, dark brown when over-mature, sessile, spongy-

thickened at base surrounding achene; adaxial veins absent or up to 10, faint; abaxial veins 5–18; serrulate on margins to 0.1–0.8 mm below base of beak. Beak 0.55–1.1 (1.35) mm, 0.25–0.55 times as long as body, serrulate on margins, toothed apically; teeth more or less blunt, 0.2–0.5 mm. Achenes 1.4–1.9 mm × 1.1–1.55 mm, ovate, biconvex, sessile; style deciduous; stigmas 2. Anthers 3, 0.7–1.3 mm. Figs. 29 (perigynia) and 39 (infructescence).

Before it was recognized and described by Mackenzie, specimens of this species were for many years identified as either *Carex atlantica* or *C. echinata*. When robust, it is an unmistakable plant with its broad leaves and dense heads of closely aggregated spikes. There are no problems of nomenclature or typification with this species.

Carex wiegandii is a rare species of restricted range. Few specimens have been examined. Nevertheless, it does not seem to be a variable species. The plant is quite uniform in appearance throughout its range.

Its relationships in the rest of the *Stellulatae* are with *Carex interior* as noted before, and to some extent, *C. atlantica*. Occasional specimens with very broad perigynia may resemble *C. atlantica* but they can usually be separated by the dense infructescence of *C. wiegandii*. As well, the perigynia of *C. wiegandii* are sometimes only faintly nerved or even nerveless on the adaxial surface. The ranges of the two species barely overlap. As *C. wiegandii* is similar in some of its features to *C. interior* it provides an interesting connection between *C. interior* and *C. atlantica*. It is possible that *C. wiegandii* may have been derived from past hybridisation of *C. interior* and a broad-leaved race of *C. atlantica*.

The range of *Carex wiegandii* is centered on the Gulf of St. Lawrence with stations sparingly inland to Ontario and south, very sparingly, to Maine, extreme northern Massachusetts, and recently discovered sites in Pennsylvania (Rothrock, 1978) (Fig. 19). It has been reported from northern New York (Mackenzie, 1931; Fernald, 1950) but no specimens have been seen from there. As it occurs in adjacent Quebec, its occurrence there is probable. Its previously unreported occurrence as far west as the Lake Superior region is interesting (Corbeil Pt. Algoma Dist. Ontario, T. M. C. Taylor et al. 438, July 26, 1935, CAN, GH; 471, July 22, 1935, CAN; 15 mi N. of Sault Ste. Marie [Algoma Dist.] Ontario, J. K. Jeglum, D. E. Harvey 3317, Aug. 7, 1970, SSMF). The species should be sought in suitable habitats elsewhere in the Lake Superior region and throughout central and eastern Canada and the northern United States.

Carex wiegandii is a plant of relatively restricted habitat. It occurs in *Sphagnum* bogs or boggy thickets and lake shores and sometimes along more open trails or ditches through bogs.

5. *Carex ruthii* Mackenzie, N. Am. Fl. 18: 112. 1931. Holotype: Craggy Mt. N. C. Albert Ruth, July 1900. NY(!).

C. muricata L. var. *ruthii* (Mackenzie) Gleason, Phytologia 4: 22. 1952.

Rhizomes short; plants caespitose; roots smooth, pale yellowish-brown to dark grey-brown; culms (23) 30–100 cm, erect, elongating in fruit, aphyllopodic, scabrous above; basal sheaths persistent, pale to dark brown. Leaves 3–7 per culm, all in basal third, more or less equalling culms in fruit; blades 30–70 cm × 1.6–5.0 mm, plicate to flat, antrorsely scabrous margined, upper blades of culm longer than lower and blades of sterile shoots longer; widest leaf (2.6) 2.9–5.0 mm. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 6–18 cm; inner band hyaline to straw coloured, sometimes purple dotted above; sheath apex concave, more or less thickened; ligule 1.0–2.5 mm; rounded. Infructescence (22) 30–85 mm, lax; spikes 3–8. Terminal spike 7–15.5 mm, staminate at base, pistillate above; staminate portion 2.0–11.0 (14.0) mm × 0.8–1.6 mm, 3–14-flowered; pistillate portion 4.1–8.0 mm × 6.1–7.7 mm, 10–25-

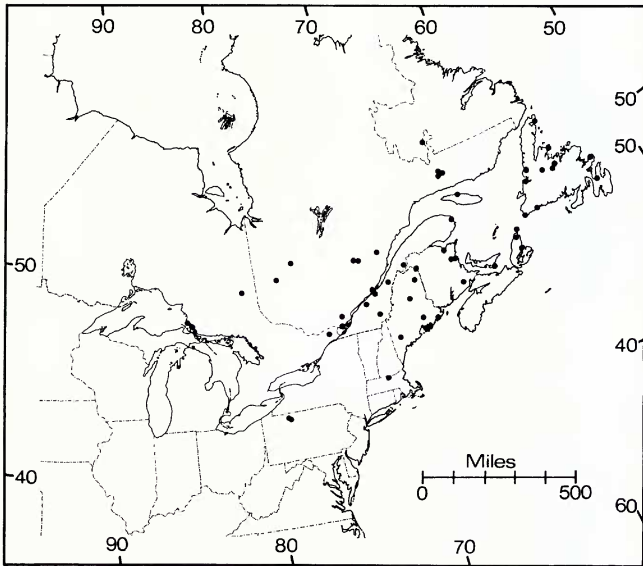


FIG. 19. Distribution of *Carex wiegandii*.

flowered. Lateral spikes 3.6–11.2 mm, sessile, pistillate or sometimes staminate at base and pistillate above; staminate portion up to 1 mm and 2-flowered; pistillate portion 3.6–11.2 mm, 6–28-flowered. Distance between upper 2 spikes 0.3–4.5 (8.0) mm, distance between lower 2 spikes (5) 10–40 mm; lateral spikes with short, scale-like bracts. Pistillate scales 1.4–2.2 mm \times 1.1–2.0 mm; ovate, one-veined, obtuse to acute, usually castaneous with green center and hyaline margins. Staminate scales 1.6–2.4 mm \times 1.1–1.9 mm; narrowly ovate, one-veined, obtuse to acute; castaneous with green center and hyaline margins. Lower perigynia of spikes spreading to reflexed, broadly to narrowly ovate, (2.8) 3.0–4.4 mm \times 1.3–1.9 (2.1) mm, (1.6) 1.8–2.5 times as long as wide, tapering to a beak, plano-convex, olive-green; sessile, spongy-thickened at base surrounding achene; adaxial nerves absent or up to 5; abaxial nerves 6–14; smooth margined below base of beak. Beak 0.9–1.75 mm, 0.43–0.85 times as long as body, serrulate on margins, toothed apically; teeth stiff, 0.15–0.35 mm. Achenes 1.1–1.8 mm \times 0.9–1.4 mm; ovate, biconvex, sessile; style deciduous; stigmas 2. Anthers 3, 0.8–1.45 mm. Figs. 30 (perigynia) and 43 (infructescence).

This restricted endemic of the southern Appalachian mountains is a striking plant with a very elongate infructescence. There are no problems in nomenclature and typification associated with it.

The few specimens examined were all very similar. The elongate infructescence combined with very broad leaves is not shown by any other species of *Stellulatae*.

Occasionally, specimens with broad perigynia may appear similar to *Carex atlantica* but the nature of the infructescence and the usually long-beaked perigynia, serrulate only on the beak, help to separate the two. Although allied by Mackenzie (1931) to *C. cephalantha* as well as to *C. atlantica* and *C. wiegandii*, it appears that its closest relative in the *Stellulatae* is *C. atlantica*. It differs from the *C. echinata* complex in its short pistillate scales, broad leaves, and elongate infructescence as well as the green colour of the perigynia.

The distribution of the species (Fig. 20) is limited to the Appalachian Mountains from southwestern Virginia to extreme northern Georgia and South Carolina. This is a distribution characteristic of many restricted Appalachian endemics such as *Diphylleia cymosa*, *Chelone lyonii*, *Pieris floribunda*, *Cymophyllus fraseri*, *Buckleya distichophylla*, and *Saxifraga careyana*. It occurs, according to herbarium labels, in moist forests, especially along trails, ditches, and streams through forests; boggy meadows and balds; and around seepage areas and springs.

6. *Carex atlantica* L. H. Bailey, Bull. Torr. Bot. Club 20: 425. 1893. Based on *C. stellulata* Gooden. var. *conferta* Chapman.

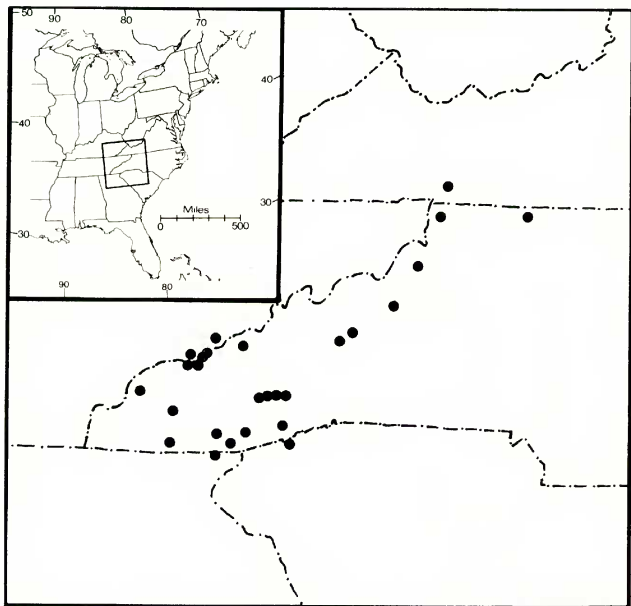


FIG. 20. Distribution of *Carex ruthii*.

- C. stellulata* Gooden. var. *conferta* Chapman, Fl. S. U.S. 534. 1860. Lectotype (*des. nobis*): Gadsden Co. Florida, Chapman. NY(!).
C. echinata Murr. var. *conferta* (Chapman) L. H. Bailey, Cat. N. Am. Carices 2. 1884.
C. incompta Bicknell, Bull. Torr. Bot. Club 35: 494. 1908. Holotype: Bog below the "Cliff," foot of the Sea Cliff Inn, Nantucket Island, Massachusetts, Eugene P. Bicknell, June 20, 1908. NY(!). Isotypes GH(!), PH(!).
C. atlantica Bailey var. *incompta* (Bicknell) F. J. Hermann, Rhodora 67: 362. 1965.

Rhizome short; plants cespitose; roots smooth, yellowish to grey-brown; culms 10–110 cm, erect to more or less spreading, elongating in fruit, aphyllopodic, scabrous margined above; basal sheaths persistent, light brownish. Leaves 3–5 per culm, all in basal third, equalling to shorter than culms in fruit; blades 8–60 cm \times 0.4–4.0 (4.5) mm, plicate, antrorsely scabrous on margins above; upper blades of culm longer than lower and blades of sterile shoots longer; widest leaf 0.8–4.0 (4.5) mm. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 3.5–24 cm; inner band hyaline, sometimes purple dotted above; sheath apex concave, more or less thickened; ligule of uppermost culm leaf 0.5–3.7 mm, rounded to obtuse. Inflorescence 8–55 mm, dense to lax; spikes 2–8. Terminal spike 4.8–23.7 mm, staminate at base, pistillate above; staminate portion 1.8–13.5 mm \times 0.8–1.3 mm, 2–21-flowered; pistillate portion 3.0–11.0 mm \times 4.4–7.5 mm, 4–38-flowered. Lateral spikes 3.1–13.1 mm, sessile, pistillate with often a few staminate flowers at base; staminate portion up to 6.5 mm and 10-flowered; pistillate portion 2.5–12 mm, 3–40-flowered. Distance between upper 2 spikes 0.6–12.5 mm, distance between lower 2 spikes 1.5–18.0 mm; lateral spikes with short, scale-like bracts. Pistillate scales 1.2–2.4 mm \times 1.2–2.0 mm, ovate to more or less suborbicular, one-veined, obtuse to more or less acute, green with hyaline margins, rarely castaneous. Staminate scales 1.3–3.5 mm \times 0.8–1.4 mm, ovate-lanceolate to ovate, one-veined, acute to obtuse, green with hyaline margins, rarely castaneous. Lower perigynia of spikes spreading to reflexed, broadly ovate to suborbicular, 1.9–3.8 mm \times 1.3–3.0 mm, 1.1–1.7 (1.9) times as long as wide, tapering to a beak, plano-convex, green, rarely more or less castaneous when first ripe, dark brown when over-mature, sessile, spongy-thickened at base surrounding achene, serrulate on margins to 0.7 mm below base of beak; adaxial veins over achene (0) 1–12; abaxial veins 6–13. Beak 0.45–1.25 mm, 0.23–0.5 (0.63) times as long as body, serrulate on margin, apex toothed; teeth stiff, 0.15–0.45 mm. Achenes 1.0–1.9 mm \times 1.0–1.7 mm, deltoid to rhombic-orbicular, biconvex, sessile; style deciduous; stigmas 2. Anthers 3, 0.6–1.5 (1.8) mm.

This is the only species of *Stellulatae* in much of the southeastern United States. Mackenzie (1931) stated that the type of *Carex stellulata* var. *conferta* Chapman was from "Apalachicola, Florida" but the specimen so labelled in herb. Chapman was called by Chapman *C. stellulata*, not *C. stellulata* var. *conferta*, and cannot be the type. The lectotype is here chosen to be a specimen labelled Gadsden Co. Florida and named *C. stellulata* var. *conferta* by Chapman.

Carex atlantica, including the subspecies *capillacea*, is a very variable species. In size it ranges from over 1 m tall with leaves up to ca. 4 mm wide to delicate plants scarcely 20 cm high with leaves less than 1 mm wide. Normally distinguished by its very broad perigynia, 1.1–1.7 times as long as wide, a very few specimens are intermediate in colour, perigynium length/width ratio, and beak length between this species and *C. echinata*. These plants may be hybrids or rare, extreme variants of *C. echinata*. Some apparently intermediate plants are found north of the range of *C. atlantica*.

The closest relatives of *Carex atlantica* are *C. echinata*, *C. ruthii*, and *C. wiedandii*. From all these species it is usually distinguishable by its broad perigynia. Its wide range in the south and its distinctive perigynium shape and colour and overall aspects indicate that it is an old species that has been able to occupy a niche no other extant species of *Stellulatae* has entered.

The distribution of *Carex atlantica* (Figs. 21, 22) covers essentially all of the eastern United States, extending very sparingly into Canada in Nova Scotia and Quebec. It is, however, clearly most abundant on the coast. Its occurrence as a disjunct at the head of Lake Michigan, in Michigan and Indiana, is, as noted with *C. seorsa*, characteristic of coastal species. Most of the range of *C. atlantica* is in unglaciated territory but it has been able to spread into wetlands in glaciated territory to some extent, although less so than *C. echinata* or *C. interior*.

The habitats of *Carex atlantica* in the north are primarily bogs and wet, acid thickets and forest edges. It does not inhabit calcareous sites. In the south, where the species is more common, it occupies, judging from herbarium labels, a wide range of wetland habitats, usually on sandy or peaty acid soil.

6a. *Carex atlantica* subsp. *atlantica*

Culms usually 25–110 cm; leaves usually 1.0–4.0 (4.5) mm wide, widest leaf usually 1.55–4.0 (4.5) mm; infructescence usually 15–55 mm with 3–8 spikes; perigynia 2.3–3.8 mm \times 1.5–3.0 mm, 1.1–1.7 times as long as wide; beak usually 0.6–1.25 mm. Figs. 31 (perigynia) and 40 (infructescences).

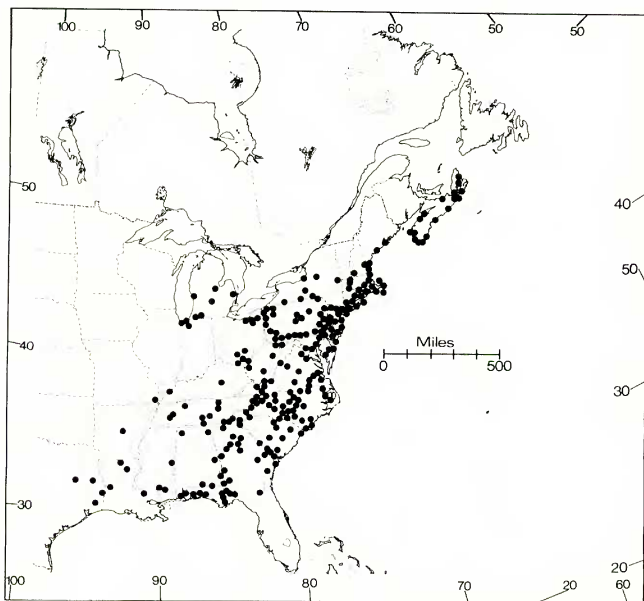


FIG. 21. Distribution of *Carex atlantica* subsp. *atlantica*.

This subspecies is the common large *Stellulatae* of the southeastern United States. Often particularly robust near the coast, the plant is also widely present inland. Its distribution is shown in Fig. 21. The possible evolutionary relationships of *C. atlantica* subsp. *atlantica* and subsp. *capillacea* are discussed under the latter subspecies.

6b. *Carex atlantica* subsp. *capillacea* (L. H. Bailey) Reznicek *comb. nov.*

C. interior L. H. Bailey var. *capillacea* L. H. Bailey, Bull. Torr. Bot. Club 20: 426. 1893. Lectotype (*des. nobis*): Arlington [Massachusetts] June 21, 1885. W. Boott. GH(!).

C. scirpoides Willd. var. *capillacea* (L. H. Bailey) Fernald, Rhodora 10: 47. 1908.

C. delicatula Bicknell, Bull. Torr. Bot. Club 35: 495. Nov. 1908. not *C. delicatula* C. B. Clarke, Kew Bull. Misc. Inf. Add. Ser. 8: 79. Aug. 1908.

C. stellulata Gooden. var. *scirpoides* (Willd.) Darlington forma *capillacea* (L. H. Bailey) Kükenthal, Das Pflanzenreich 4: 20. 231. 1909.

C. howei Mackenzie, Bull. Torr. Bot. Club 37: 245. 1910. Based on *C. interior* L. H. Bailey var. *capillacea* L. H. Bailey.

C. mohriana Mackenzie, N. Am. Fl. 18: 106. 1931. Holotype: Swamp near Wauchula, S. Florida, A. H. Curtiss 6761, Apr. 15, 1901. GH(!). Isotypes QK(!), UC(!), MIN(!), MICH(!).

The smallest extreme of *C. atlantica*. Culms usually 10–60 cm; leaves 0.4–1.55 mm wide; widest leaf (0.65) 0.8–1.55 mm; infructescence usually 8–20 mm long with 2–5 spikes; perigynia 1.9–3.0 mm X 1.3–2.0 mm, (1.15) 1.3–1.7 (1.9) times as long as wide; beak 0.45–0.95 mm. Figs. 32 (perigynia) and 41 (infructescence).

This taxon was long known as *Carex howei* or *C. interior* var. *capillacea*. Its affinities have been shown above to be with *C. atlantica*, with which it in fact intergrades. Bailey (1893) described *C. interior* var. *capillacea* from "Eastern Massachusetts, New Jersey and central Pennsylvania." Mackenzie (1931) states "specimens collected in eastern Massachusetts by Wm. Boott, who first called attention to the plant, are taken as the type of *C. interior* var. *capillacea* . . ." Of several specimens from Boott's herbarium, all presumably seen by Bailey, "Arlington, June 21, 1885 W. Boott" (GH) is selected as the lectotype.

This delicate sedge is quite distinct in some parts of its range, especially north of the glacial boundary as pointed out earlier, but plants grading imperceptibly into *Carex atlantica* subsp. *atlantica* are not infrequent over much of the range of the species. Thus, recognition at subspecific level seems much more to represent the evolutionary relationships of the taxon. The area south of the glacial boundary and inland from the coastal plain is the oldest part of the species range. *Carex atlantica* presumably migrated from there onto the outer coastal plain and newly deglaciated territory as these areas became open for colonization. Differentiation accompanied migration until the frequencies of occurrence of character states are quite different in these different areas. The segregation is most pronounced in the northeast of the species' range where *Carex atlantica* subsp. *atlantica* and subsp. *capillacea* are quite distinct and may grow together without intergrading. *C. atlantica* subsp. *capillacea* is likely an incipient species, as yet only partially differentiated. The range of the taxon is from Nova Scotia to Texas along the Atlantic Coast and locally inland in New York, Pennsylvania, Quebec, Ohio, and Michigan as shown in Fig. 22.

7. *Carex echinata* Murray, Prod. Stirp. Gott. 76. 1770. Lectotype (*des. nobis*): plate 284, Flora Danica (Oeder, 1766).

C. leersii Willdenow, Fl. Berol. Prod. 29. 1787. *Nom. Illeg.*

C. stellulata Goodenough, Trans. Linn. Soc. 2: 144. 1794. Type not traced.

C. stellulata Gooden. var. *angustata* Carey, Carices N. U.S. 544. 1847. Lectotype (*des. nobis*): Fairfield, New York, K. Photo TRTE(!). Isolectotype GH(!).

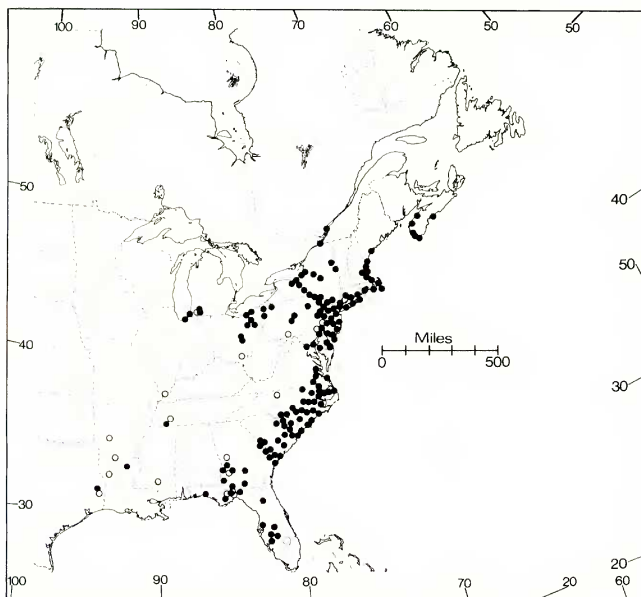


FIG. 22. Distribution of *Carex atlantica* subsp. *capillacea*. Open circles indicate intermediates with *C. atlantica* subsp. *atlantica*.

C. echinata Murr. var. *cephalantha* L. H. Bailey, Mem. Torr. Bot. Club 1: 58. 1889. Lectotype (*des. nobis*): Ashland, Mass. June, 1879, Thomas Morong. (GH)(!).

C. echinata Murr. var. *angustata* (Carey) L. H. Bailey, Mem. Torr. Bot. Club 1: 59. 1889.

C. sterilis Willd. var. *angustata* (Carey) L. H. Bailey, Bull. Torr. Bot. Club 20: 425. 1893.

C. sterilis Willd. var. *cephalantha* (L. H. Bailey) L. H. Bailey, Bull. Torr. Bot. Club 20: 425. 1893.

C. sterilis Willd. var. *excelsior* L. H. Bailey, Bull. Torr. Bot. Club 20: 424. 1893. Holotype: Junius, New York, No. 35, H. P. Sartwell, Carices Americae Septentrionalis Exsiccatae, Pars 1, 1848. (GH)(!). Isotype NY(!).

C. sterilis Willd. var. *aequidistans* Peck ex E. C. Howe, Ann. Rep. N.Y. State Mus. 48: 137. 1897. Type locality: Oneida and Essex Counties, N.Y. Type not traced.

C. echinata Murr. var. *ormantha* Fernald, Proc. Am. Acad. Arts Sci. 37: 483. 1902. Lectotype (*des. Mackenzie*): Bog along Strawberry Creek, Sierra Nevada Mts., El Dorado Co., California, Ezra Brainerd 160, July 18, 1897. (GH)(!).

C. echinata Murr. var. *excelsior* (L. H. Bailey) Fernald, Proc. Am. Acad. Arts Sci. 37: 484. 1902.

C. stellulata Gooden. var. *ormantha* (Fernald) Fernald, Rhodora 4: 222. 1902.

C. stellulata Gooden. var. *cephalantha* (L. H. Bailey) Fernald, Rhodora 4: 222. 1902.

C. stellulata var. *excelsior* (L. H. Bailey) Fernald, Rhodora 4: 222. 1902.

C. interior L. H. Bailey var. *josselynii* Fernald, Rhodora 8: 115. 1906. Holotype: Wet sandy river-bank, Fort Kent, Valley of the St. John River, Aroostook Co., Maine, M. L. Fernald, July 6, 1904. (GH)(!). Isotypes NY(!), MICH(!, fragment).

- C. scirpoides* var. *josselyinii* (Fernald) Fernald, *Rhodora* 10: 48. 1908.
C. cephalantha (L. H. Bailey) Bicknell, *Bull. Torr. Bot. Club* 35: 493. 1908.
C. stellulata Gooden. var. *sterilis* (Willd.) Carey forma *excelsior* (L. H. Bailey) Kükenthal, *Das Pflanzenreich* 4: 20. 231. 1909.
C. leersii Willd. var. *angustata* (Carey) Mackenzie ex Small & Carter, *Fl. Lancaster Co.* 55. 1913.
C. leersii Willd. var. *cephalantha* (L. H. Bailey) J. K. Henry, *Fl. S. Brit. Col.* 60. 1915.
C. angustior Mackenzie in Rydberg, *Fl. Rocky Mts. Adj. Plains Ed.* 1. 124. 1917.
C. ormantha (Fernald) Mackenzie, *Erythraea* 8: 35. 1922.
C. josselyinii (Fernald) Mackenzie ex Pease, *Proc. Bost. Soc. Nat. Hist.* 37: 188. 1924.
C. muricata L. var. *cephalantha* (L. H. Bailey) Wiegand & Eames, *Cornell Univ. Agr. Exp. St. Mem.* 92: 120. 1926.
C. laricina Mackenzie ex Bright, *Trillia* 9: 4. 1930. Holotype: Presque Isle, low wet, sandy, back shores. June 16, 1927. John Bright. Location of type not known.
C. angustior Mack. var. *gracilentata* Clausen & Wahl, *Rhodora* 41: 30. 1939. Holotype: Moist woodland along stream at Ingleby, 2 mi. east of Coburn, Centre Co., Pennsylvania, R. T. Clausen and H. A. Wahl 2532, June 6, 1937. GH(!). Isotypes CU n.v., BH n.v.
C. muricata L. subsp. *cephalantha* (L. H. Bailey) Clausen, *Cornell Univ. Agr. Exp. St. Mem.* 291: 10. 1949.
C. muricata L. var. *angustata* (Carey) Gleason, *New Britton and Brown Illus. Fl.* 1: 318. 1952.
C. muricata L. var. *laricina* (Bright) Gleason, *Phytologia* 4: 22. 1952.
C. phyllomanica W. Boott var. *angustata* (Carey) Boivin, *Phytologia* 43: 51. 1979.
C. phyllomanica W. Boott var. *ormantha* (Fernald) Boivin, *Phytologia* 43: 51. 1979.

Rhizomes short; plants caespitose; roots smooth, yellowish to brown; culms 10–90 (135) cm, erect to more or less spreading, elongating in fruit, aphyllopodic, scabrous on margins above; basal sheaths persistent, light brown. Leaves 3–6 per culm, all in basal third, shorter than to equalling culms in fruit; blades 5–40 cm × 0.7–3.3 (3.8) mm, plicate, antrorsely scabrous on margins above; upper blades of culm longer than lower and blades of sterile shoots much longer; widest leaf 1.0–3.3 (3.8) mm. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 1.8–2.5 cm; inner band hyaline, sometimes purple dotted above; sheath apex concave, scarcely thickened; ligule of uppermost culm leaf 0.6–2.5 (4.5) mm, rounded to more or less acute. Inflorescence 7–78 mm, dense to very lax; spikes (2) 3–8. Terminal spike 5.0–24.0 mm, staminate at base, pistillate above; staminate portion 2.0–16.5 mm × 0.9–2.0 mm, 2–17-flowered; pistillate portion 2.6–9.0 mm × 4.9–9.1 mm, 4–26-flowered. Lateral spikes 3.0–15.5 mm, sessile, pistillate with often a few staminate flowers at base; staminate portion up to 8.2 mm and 7-flowered; pistillate portion 2.5–11 mm, 3–32-flowered. Distance between upper 2 spikes 0.6–14.5 mm, distance between lower 2 spikes 1.7–42.0 mm; lateral spikes with short, scale-like bracts. Pistillate scales 1.4–3.1 mm × 0.7–2.3 mm, ovate, one-veined, acute to sometimes obtuse, castaneous with green center and hyaline margin. Staminate scales 1.3–3.8 mm × 0.8–1.7 mm, ovate-lanceolate to ovate, one-veined, acute, castaneous with green center and hyaline margins. Lower perigynia of spike spreading to reflexed, lanceolate to ovate, (2.65) 2.85–4.75 mm × 0.8–2.1 mm, (1.7) 1.8–3.2 (3.6) times as long as wide, tapering to a beak, plano-convex, green to castaneous when first ripe, dark brown when over-mature, sessile, spongy-thickened at base surrounding achene, serrulate on margins to 0.85 mm below beak; adaxial veins over achene none or up to 12; abaxial veins 2–14. Beak 0.85–2.0 mm, (0.4) 0.45–0.86 times as long as body, serrulate on margins, apex usually toothed, teeth stiff, sharp (0) 0.15–0.5 mm. Achenes 1.3–2.1 mm × 0.8–1.55 mm, ovate-lanceolate to rhombic ovate, biconvex, sessile; style deciduous; stigmas 2. Anthers 3, 0.8–1.6 (2.0) mm.

Synonymy given for this species includes only names that have been widely used in North America or are based on North American types. Complete synonymy, including names of varieties and forms, is found in Kükenthal (1909) and Mackenzie (1931).

The correct name for this widespread species has been the subject of much dispute. Four names have been applied with some regularity: *Carex muricata* Linnaeus (1753), *C. echinata* Murray (1770), *C. leersii* Willdenow (1787), and *C. stellulata* Goodenough (1794).

Mackenzie (1923) argued for the applicability of the name *Carex muricata* L. He noted that the plant was described by Linnaeus (1745) in his "Flora Suecica" and the description was nearly the same as in the later "Species Plantarum." This plant, he argued, grew in wetlands and Mackenzie (1923) stated "there never has been any doubt that the plant of wet places, which occurs especially in north Sweden and which is, undoubtedly to be taken as, the type of *Carex muricata* is the same as *Carex stellulata* L. [sic]." He noted that "the botanists immediately following Linnaeus seem to have been quite unanimous in applying the name *Carex muricata* to what has in more recent times usually been called *Carex stellulata* Good." However, Mackenzie did not mention that Goodenough (1794), in describing *C. stellulata*, noted at that early date that the botanists immediately following Linnaeus were in error in their application of this name and that the Linnaean herbarium confirmed this. Mackenzie (1923) dismissed the Linnaean herbarium by noting that Kükenthal (1909) stated that there was a mixture in Linnaeus' specimens. On that basis, Kükenthal in fact rejected the name *C. muricata* altogether. However, when the Linnaean herbarium is consulted, there is found a sheet labelled "8 *muricata*." The name and number directly connect that sheet with the name and number in Species Plantarum Ed. 1. The other sheet in the Linnaean herbarium, the basis of Kükenthal's (1909) "mixture," is unnamed and has no bearing on the application of the name *C. muricata*. The Linnaean plant clearly has androgynous spikes and is a member of the section *Bracteosae*. Mackenzie's arguments, based on pre-1753 literature, are not to the point. At best, Mackenzie could have shown that Linnaeus had changed his mind between Flora Suecica and Species Plantarum Ed. 1. As has been pointed out by David (1976), there can be no confusion as to the application of the name *C. muricata* L. Continued use of the name for species of *Stellulatae* by recent authors (Gleason, 1952; Gleason and Cronquist, 1963; Boivin, 1967; Hitchcock and Cronquist, 1973) is incorrect.

Carex echinata Murray (1770) was based on a description by Haller (1768) and plate 284 of "Flora Danica" (Oeder, 1766). Haller (1768) also refers to Oeder's illustration. Haller's description and Oeder's plate are clearly the common "Star Sedge" of Europe. Oeder's plate is designated the lectotype of *C. echinata* Murray.

Fernald (1902) noted, quoting a letter from C. B. Clarke, that "*C. echinata* Murr. is = *C. divulsa* Gooden. and not near *C. stellulata* Gooden. The original sheet of Murray is in the British Museum, inscribed in his own hand as his *echinata*; it is a very good specimen and Jas. Britten (or any other botanist at the British Museum) will tell you that there can be no dispute about this identification." However, Murray's new name was validated by his citation of Haller's (1768) polynomial epithet and the typification must be based on Haller's work. Murray's specimen is irrelevant to the selection of a type. This same case has been argued by Britten (1907), Kovacs (1910), Briquet (1910), Fernald (1917), de Langhe (1944), and David (1976) who all concurred with this application of the name *C. echinata*. The use of the name *C. echinata* for a member of the *Bracteosae*, as has been done by Kükenthal (1905, 1909), is in error.

Carex leersii Willdenow (1787) was clearly described and there is no doubt his name applies to the plant previously named *C. echinata*. However, since Willdenow cited the type of *C. echinata*, his name is illegitimate. *Carex stellulata* Goodenough was also clearly described and applies to *C. echinata* but is a later synonym. There can be no doubt that the correct name for the species in question here is *C. echinata* Murray.

Carex echinata, including the robust, coastal subspecies *phyllomanica*, is the most variable species of *Stellulatae* in North America. It ranges in height from 10 to rarely over 90 cm; the perigynia vary from slightly under 3 to well over 4 mm in length and in shape from lanceolate to more or less broadly ovate. The infructescence may be very lax and open to quite compact. Furthermore, as discussed previously, variations in these and other characters are often only loosely correlated with each other. As well, a large portion of the variation is expressed in Europe.

Carex echinata is most similar to *C. atlantica* and *C. interior*. Its separation from these two species and the occurrence of rare intermediates has been discussed under these species.

At present, the range of *Carex echinata* is essentially divided into two parts in North America (Figs. 23, 24). Although *C. echinata* is most abundant and robust near the east and west coasts, the virtual absence of the species in the boreal region of the center of North America may well be due to the species having been eliminated by Pleistocene glaciation. Its absence in the center of boreal North America is paralleled by its apparent absence from the center of boreal Russia (Egorova, 1960). In western North America, the species likely survived glaciation in the southern mountains, along the southern coast, and perhaps in coastal refugia northwards as discussed by Calder and Taylor (1968). In the east, it survived also in the southern mountains and along the southern coast. It is here postulated that the species is still actively migrating and, in future millennia, will colonize the boreal region of northern Canada and have a continuous distribution across the continent.

The splitting of the species range into parts during the glacial maximum is probably at least partly responsible for the great variability of the taxon. Also, as the species migrated into new territory after deglaciation, the migration was accompanied by further differentiation. As suggested earlier, the species is probably still actively migrating and evolving at the present. One of the consequences of this is the taxonomic difficulty of the *C. echinata* complex.

Carex echinata is primarily a species of acidic wetlands such as *Sphagnum* bogs, peaty or sandy lake and river shores, boggy meadows, and openings in coniferous forest. Along the northeast coast of North America, where the species is especially common, it may grow in roadside ditches, wet pastures and meadows, and even as a weed in commercial cranberry bogs.

7a. *Carex echinata* subsp. *echinata*

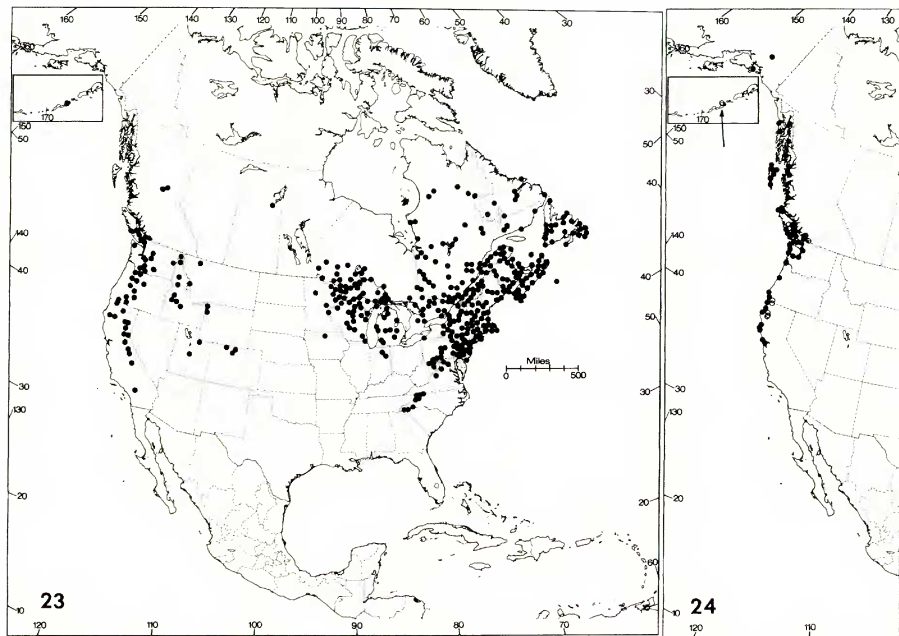
Culms 10–90 (135) cm; leaves usually 0.7–2.7 (3.3) mm wide; widest leaf 1.0–2.7 (3.3) mm wide; infructescence 7–78 mm, lax to dense; perigynia (2.65) 2.85–3.6 (4.6) mm, nerved or not over achene on adaxial surface; often serrulate on margins below base of beak. Figs. 33 (perigynia) and 44 (infructescences).

This widespread subspecies is abundant and variable throughout all the range shown in Fig. 23, except that it is largely replaced on the west coast of North America by *Carex echinata* subsp. *phyllomanica*. It is also widespread in Europe. The exact taxonomic disposition of Asiatic and southern hemisphere representatives of the *C. echinata* complex is not known.

7b. *Carex echinata* subsp. *phyllomanica* (W. Boott) Reznicek *comb. nov.* *C. phyllomanica* W. Boott in Watson, Bot. Calif. 2: 233. 1880. Holotype: In swamps, Mendocino City, California. H. N. Bolander 4746, 1866. GH(!). Isotypes NY(!), UC(!).

Culms 20–80 cm; leaves 1.0–3.3 (3.8) mm wide; widest leaf (1.7) 2.3–3.3 (3.8) mm wide; infructescence 12–25 (40) mm, very dense; distance between lower 2 spikes usually less than length of lowest spike; perigynia (3.1) 3.5–4.75 mm; usually 2–12 nerved over achene on adaxial surface; usually not serrulate below base of beak. Figs. 34 (perigynia) and 42 (infructescence).

This striking, broad-leaved western coastal race is distinctive in its extreme but forms that intergrade with *Carex echinata* subsp. *echinata* are scattered throughout its



FIGS. 23–24. Distribution of *Carex echinata*. 23. *C. echinata* subsp. *echinata*. 24. *C. echinata* subsp. *phyllomanica*. Open circles indicate intermediates with *C. echinata* subsp. *echinata*.

range, especially somewhat inland from the coast. It is widespread from Santa Cruz County, California (Munz, 1959) to the coastal regions of Alaska east of Prince William Sound (Fig. 24). It is especially robust and abundant on the Olympic peninsula, Washington, Vancouver Island, and the Queen Charlotte Islands. It occurs in bogs and along streams and lakeshores in the coastal forests.

8. *Carex seorsa* E. C. Howe in Gordinier & E. C. Howe, Fl. Renss. Co. N.Y. 39. 1894. Holotype: Border of shaded swamp, Lansings' Grove, Lansingburgh, N.Y. E.C. H[owe], May 1866. NYS n.v. Isotype NY(!).

C. rosaeoides E. C. Howe in Gordinier & E. C. Howe, Fl. Renss. Co. N.Y. 33. 1894. Not validly published. Name rejected by author; *C. seorsa* was substituted for it in same publication.

Rhizomes short; plants cespitose; roots smooth, yellowish to brown; culms 15–75 cm, erect to more or less spreading, elongating in fruit, aphyllopodic, smooth; basal

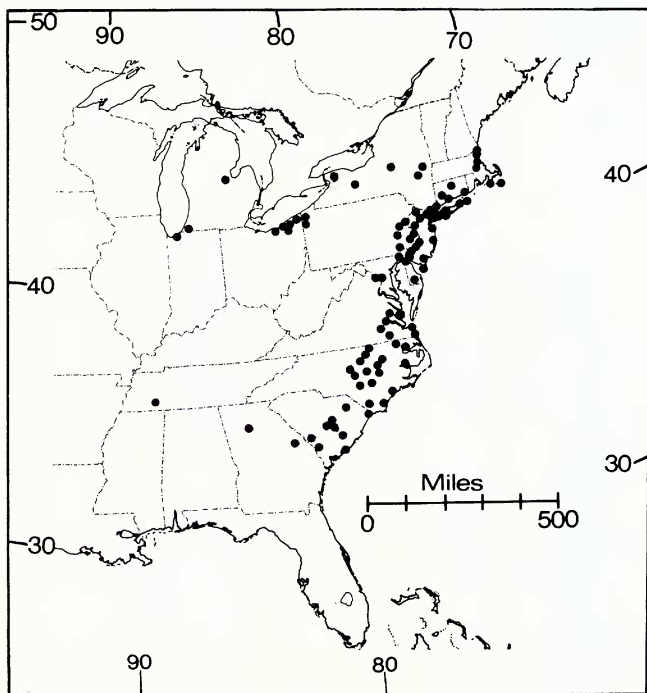
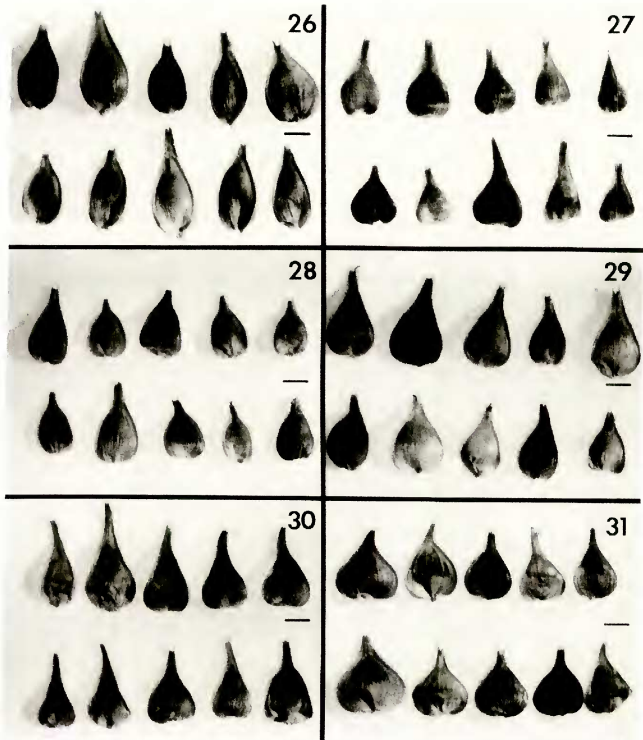


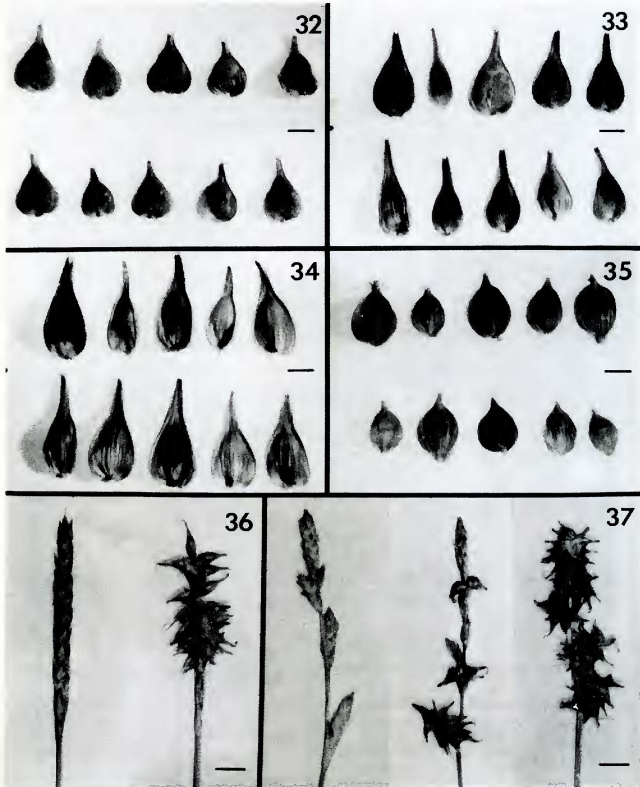
FIG. 25. Distribution of *Carex seorsa*.



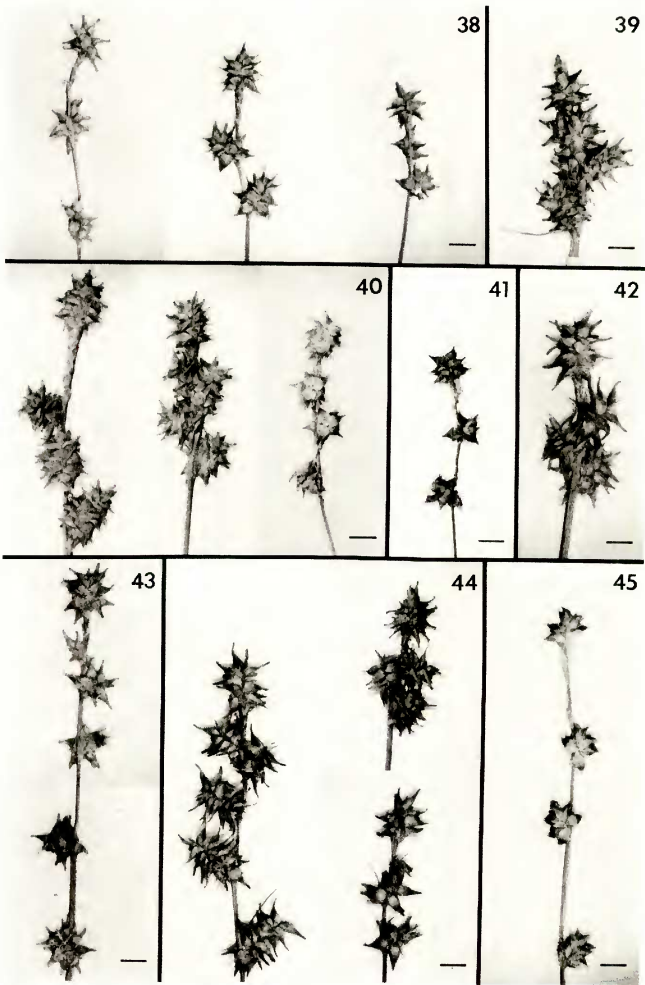
FIGS. 26–31. Variation in perigynia of *Carex*. 26. *C. exilis*. 27. *C. sterilis*. 28. *C. interior*. 29. *C. wiegandii*. 30. *C. ruthii*. 31. *C. atlantica* subsp. *atlantica*. The bar equals 1 mm in all figures.

sheaths persistent, light brown. Leaves 2–4 per culm, all in basal third, usually shorter than culms in fruit; blades 9–50 cm \times 0.8–3.9 mm, plicate to flat, antrorsely scabrous on margins above, upper blades of culm longer than lower and blades of sterile shoots longer; widest leaf 2.1–3.9 mm. Sheaths covering nodes, tight, glabrous, that of uppermost leaf 3.5–12 cm; inner band hyaline; sheath apex deeply concave, not thickened; ligule 1.7–7.0 mm, acute or often with an emarginate apex. Inflorescence 18–70 mm, lax; spikes 4–8. Terminal spike 4.7–16.5 mm, staminate at base, pistillate above; staminate portion 1.8–12.7 mm \times 0.9–2.1 mm, 3–13-flowered; pistillate portion 2.8–7.3 mm \times 4.4–6.0 mm, 6–23-flowered. Lateral spikes 2.8–10.8 mm sessile, pistillate with often a few staminate flowers at base; staminate portion (0) 0.8–4.6 mm, (0) 1–6-

flowered; pistillate portion 2.0–7.6 mm, 4–25-flowered. Distance between upper 2 spikes 0.6–5.5 mm, distance between lower 2 spikes 5–27 mm; lateral spikes with short, scale-like bracts. Pistillate scales 1.2–2.2 mm \times 1.0–1.6 mm, ovate, one-nerved, acute, green with hyaline margins. Staminate scales 1.7–3.3 mm \times 1.0–1.4 mm, ovate, one-veined, acute, green with hyaline margins. Lower perigynia of spikes spreading to reflexed, elliptic to elliptic-ovate, 1.8–2.9 mm \times 1.0–1.9 mm, 1.2–2.1 times as long as



FIGS. 32–37. Variation in perigynia and infructescences of *Carex*. 32. *C. atlantica* subsp. *capillacea*. 33. *C. echinata* subsp. *echinata*. 34. *C. echinata* subsp. *phyllomanica*. 35. *C. seorsa*. 36. *C. exilis*. 37. *C. sterilis*. The bar equals 1 mm in Figs. 32–35 and 3 mm in Figs. 36 and 37.



FIGS. 38-45. Inflorescences of *Carex*. 38. Variation in inflorescences of *C. interior*. 39. Typical inflorescence of *C. wiegandii*. 40. Variation in inflorescences of *C. atlantica* subsp. *atlantica*. 41. Typical inflorescence of *C. atlantica* subsp. *capillacea*. 42. Typical inflorescence of *C. echinata* subsp. *phyllomanica*. 43. Typical inflorescence of *C. ruthii*. 44. Variation in inflorescences of *C. echinata* subsp. *echinata*. 45. Typical inflorescence of *C. seorsa*. The bar equals 3 mm in all figures.

wide, tapering to a beak, plane-convex, green when ripe, brownish when over-mature, sessile, spongy-thickened at base surrounding achene, not serrulate on margins; adaxial nerves over achene absent or up to 6; abaxial nerves 6–14. Beak 0.2–0.6 mm, 0.09–0.33 times as long as body, smooth margined, apex truncate or obscurely blunt-toothed to 0.2 mm. Achenes 1.2–1.6 mm × 0.85–1.4 mm, ovate to orbicular, biconvex, sessile; style deciduous; stigmas 2. Anthers 3, 1.0–1.9 mm. Figs. 35 (perigynia) and 45 (infructescence).

The nomenclature and typification of *Carex seorsa* is straightforward. The name *C. rosaeoides* is not validly published as it was not accepted by the author when published (Stafleu, Voss et al. 1978, Art. 34. 1).

Carex seorsa is isolated in the *Stellulatae* with no near relatives. It is easy to separate from all other species and no intermediates are known. The species is very uniform throughout its range and no infraspecific taxa have been proposed.

The species is more or less restricted to the coastal plain in the south of its range but has penetrated newly glaciated territory to some extent in the north from northern Massachusetts to eastern Ohio (Fig. 25). The disjunct stations mapped near the head of Lake Michigan in Michigan and Indiana are characteristic of many more coastal species (Peattie, 1922; Voss, 1972).

Carex seorsa is somewhat different from the rest of the *Stellulatae* in its ecology. It is primarily a wet forest species. It appears to occur frequently on forest edges but is not a species of open wetlands.

Nomen Dubium

Carex echinata Murr. var. *microstachys* Boeckeler, Linnaea 39: 125. 1875.

The type of this variety was in the Berlin Herbarium (B) and was destroyed during World War II. The range of the taxon was given as "America borealis." There is no possibility of being certain of the application of this name from the description. It was placed by Mackenzie (1931) in synonymy with *Carex angustior*.

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